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TAXONOMY AND GEOGRAPHY OF *ROUSETTUS AMPLEXICAUDATUS* (GEOFFROY, 1810) WITH COMPARATIVE NOTES ON SYMPATRIC CONGENERS (MAMMALIA, MEGACHIROPTERA)

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ABSTRACT

Rousettus amplexicaudatus (Geoffroy, 1810) is divided into three subspecies according to size: *R. a. amplexicaudatus*, *R. a. infumatus* (Gray, 1870), and *R. a. brachyotis* (Dobson, 1877). *Cynonycteris minor* Dobson, 1873 is synonymized with *R. a. infumatus*; *Rousettus stresemanni* Stein, 1933 with *R. a. amplexicaudatus*; and *Rousettus amplexicaudatus hedigeri* Pohle, 1952 with *R. a. brachyotis*. Geography and dimensional variations of the recognized subspecies are discussed. *R. amplexicaudatus* is recorded for the first time from Celebes, Kisar, Mentawai, Muna and Ndao. The subspecific status of specimens from Celebes, Muna, Peleng and Talisai is left undecided.

Other *Rousettus* species are discussed in so far as they are known to be sympatric with certain *R. amplexicaudatus* populations: *R. leschenaultii* (Desmarest, 1820) — recorded for the first time from Bali and Simeulue —, *R. celebensis* Andersen, 1907, and *R. spinalatus* Bergmans & Hill, 1980 — of which a fourth specimen, from a new locality on Borneo, is described.

Some dental anomalies and some ectoparasities are listed.

INTRODUCTION

Étienne Geoffroy-St. Hilaire (1810) described the first species presently included in the fruit bat genus *Rousettus* Gray, 1821, his *Pteropus amplexicaudatus* from Timor. The closely related "*Pteropus Leschenaultii*" from the surroundings of Pondicherry (South-East India) was named by Desmarest (1820). Most later work on Asian representatives of *Rousettus* consists of incidental descriptions of new species (11, since 1820) and accidental extensions of their recorded ranges. Gray (1870) catalogued the fruit bats in the British Museum (Natural History) and distinguished (besides *amplexicaudatus* and *leschenaultii*) three new species in South-East Asia on the basis of colour: *Eleutherura* (= *Rousettus*) *fuli-*

ginosa (Thailand), *E. infumata* (Flores) and *E. philippinensis* (Manilla). Later in the 1870's, Gray's classification was revised by Dobson, who synonymized *leschenaultii*, *fuliginosa*, *infumata* and *philippinensis* with *amplexicaudatus* (Dobson, 1876 and 1878b) and proposed two new species, *Cynonycteris* (= *Rousettus*) *minor* from Java (Dobson, 1873) and *C. brachyotis* from Duke of York Island, Bismarck Archipelago (Dobson, 1877). In his concept, *Cynonycteris amplexicaudata* would occur "from the Persian Gulf ... to Timor". His inclusion, in this taxon, of *leschenaultii*, possibly caused by its similar forearm length, is curious because Peters (1873) had just published a long list of differences between the types of *amplexicaudatus* and *leschenaultii*. Nevertheless,

Dobson's arrangement was generally followed for some time (e.g. Jentink, 1887 and 1888; Thomas, 1894; Matschie, 1899).

Seabra (1898) described *Cynonycteris bocagei*, which would occur on Timor side by side with *C. amplexicaudatus*, and differ in the form of the palate and in zygomatic width. A second Javanese form, *Rousettus shortridgei*, was described by Thomas & Wroughton (1909). This assumedly rare species was larger than *R. minor* and "closely allied to the continental *R. leschenaultii*". Andersen (1907) erected *Rousettus celebensis*, based on a distinct specimen collected on Celebes. In 1912, Andersen published his classic revision of the fruit bats, which still provides the basis for all taxonomic research on this group. His treatment of the Asian members of the genus *Rousettus* is essentially in agreement with Dobson (1878b), with the addition of the new species described in the meantime. *R. leschenaultii*, however, is again separated from *R. amplexicaudatus*, in which Anderson & de Winton (1902) were followed, and Seabra's *C. bocagei* is synonymized with the sympatric *R. amplexicaudatus*. In an addendum included in the same work, Andersen (1912) reported on a larger series of *R. minor*, and decided to reduce *amplexicaudatus*, *minor* and *brachyotis* to subspecific level. His final arrangement of the species and his indication of their ranges may be summarized here as follows: *R. leschenaultii* ("Himalayas ... eastward through Bengal, Burma, Siam (Laos Mts.) to S. China (Amoy)"); *R. shortridgei* ("Java"); *R. celebensis* ("Celebes, Sanghir Islands"); *R. a. amplexicaudatus* ("Cambodia, Philippines, Borneo, Sumatra, Engano, Flores, Savu, Alor, Timor"); *R. amplexicaudatus minor* ("Java") and *R. amplexicaudatus brachyotis* ("Amboina, New Guinea, Bismarck Archipelago, Solomon Islands").

Only a few changes and additions have been proposed since Andersen's classification of 1912. *R. shortridgei* was taken to be a subspecies of *R. leschenaultii* by Chasen (1940) and later authors. Stein (1933) described *Rousettus stresemanni* from Japen Island (North-West of New Guinea), a species said to be only remotely related to *R. amplexicaudatus*. The form, however, was found indistinguishable from specimens of the

latter species from the New Guinean mainland by Koopman (1979). According to him, *R. amplexicaudatus stresemanni* would differ in size from the subspecies *brachyotis* of the Bismarck Archipelago, but he does not state how specimens from the Moluccas (included in *brachyotis* by Andersen) should now be classified. Pohle (1953) named the smallest form yet known, *R. a. hedigeri* from Bougainville and possibly from the southern Solomon Islands. Recently, Bergmans & Hill (1980) described *Rousettus spinalatus*, a species with a very high wing insertion, occurring on Sumatra and Borneo.

When Bergmans compared the two Sumatran type specimens of *R. spinalatus* with *R. amplexicaudatus* from different localities, it appeared that the variability and range of the latter had remained practically uninvestigated since Andersen's *magnum opus* (1912). The results of a comparative study of large numbers of available specimens of *R. amplexicaudatus*, intended to bring some light in matters like its intraspecific variation, the tenability as such of the characters used to separate the currently recognized subspecies, and the distribution of the species and its possible races, are presented in this paper.

In the museum collections in Amsterdam, Berlin, Calcutta, Leiden, London and Utrecht, specimens of other *Rousettus* species collected from North-East India towards the east, i.e. the area from where *R. amplexicaudatus* has been reported, were studied along with specimens of the latter species. Some data on these species (*R. leschenaultii*, *R. celebensis*, and *R. spinalatus*) are also given, mainly to show their distinctness from *R. amplexicaudatus*.

ABBREVIATIONS

| | |
|------|--|
| AMNH | American Museum of Natural History, New York |
| BBM | Bernice P. Bishop Museum, Honolulu |
| BMNH | British Museum (Natural History), London |
| FMNH | Field Museum of Natural History, Chicago |
| HZM | Harrison Zoological Museum, Sevenoaks |
| IMR | Institute for Medical Research, Kuala Lumpur |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| MNM | Magyar Nemzeti Muzeum, Budapest |
| MSNG | Museo Civico di Storia Naturale „Giacomo Doria", Genova |
| MVZ | Museum of Vertebrate Zoology, University of California, Berkeley |

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| MZB | Museum Zoologicum Bogoriense, Bogor |
| NHMB | Naturhistorisches Museum, Basel |
| NMW | Naturhistorisches Museum, Vienna |
| RMNH | Rijksmuseum van Natuurlijke Historie, Leiden |
| USNM | United States National Museum, Washington |
| ZMA | Zoologisch Museum, Amsterdam |
| ZMB | Zoologisches Museum, Berlin |
| ZMU | Zoologisch Museum, Utrecht |
| ZRCS | Zoological Reference Collection, University of Singapore, Singapore |
| ZSI | Zoological Survey of India, Calcutta. |

SPECIMENS EXAMINED

Of *Rousettus amplexicaudatus*, 271 skulls, 184 dry skins and 101 alcohol specimens have been studied; of *R. leschenaultii* (including *R. l. shorridgei*), 102 skulls, 52 dry skins and 31 alcohol specimens; of *R. celebensis*, 29 skulls and 33 dry skins; of *Rousettus spinalatus*, 1 alcohol specimen with extracted skull.

With the following exceptions, the specimens have been examined by the first author: those in the BMNH collection (except the type specimens) and the HZM collection were studied by the second author. Type specimens in the BMNH collection were kindly measured by Dr. J. E. Hill. Specimens in the MZM collection have been measured by Drs. G. H. Glas.

(Ad. = adult; juv. = juvenile; alc. = alcohol specimen.)

Rousettus amplexicaudatus (Geoffroy, 1810)

Alor. "Alor": 1 ad. ♂, 1 ad. ♀, skins, skulls, A.

Everett, III-1897 (BMNH 1898.11.3.20-21).

Ambon. "Amboina": 1 juv. ♂, alc. (without skull), Semon, 21-XII-1893 (ZMB 22222); 2 subad. (sex?), skulls, Semon (ZMB 66519, -22).

Bagabag. Bagabag Island: 2 ad. ♂♂, 2 ad. ♀♀, skulls, J. M. Diamond, VI-1969 (AMNH 221410-12, -16).

Bali. Oeboed, 205 m: 1 ad. ♂, 2 ad. ♀♀, skins, skulls, V. v. Plessen, 27-XII-1937 (AMNH 107438-40); 2 subad. ♀♀, skulls, V. v. Plessen, 26/27-XII-1937 (ZMB 90419-20). Selat, 600 m: 1 ad. ♂, 2 ad. ♀♀, 1 subad. ♀, skins, skulls, V. v. Plessen, 4-I-1938 (AMNH 107441-2, ZMB 92017-18). Soka: 1 ad. ♂, skin, skull, V. v. Plessen, 8-I-1938 (AMNH 107846).

Bismarck Archipelago. Emirau Island: 1 ad. ♀,

skull, C. G. Sibley, 24-VIII-1944 (MVZ 109744). Duke of York Island: 1 ad. ♀, skin, skull (holotype of *Cynonycteris brachyotis* Dobson, 1877; BMNH 1877.7.18.3); 1 ad. ♂, skin, skull (BMNH 1878.2.5.5). Neu Lauenburg (= Duke of York): 1 ad. ♀, skin, skull, Gerard (ZMB 5357). New Britain: Kandrian: 1 ad. ♂, 2 subad. ♂♂, 2 ad. ♀♀, 1 juv. ♀, skins, skulls, M. Gilliard, 31-I/4-II-1959 (AMNH 194281, -83-87). Tabar Island: 1 ad. ♂, 1 ad. ♀, skins, skulls, W. F. Coultas, 21/27-I-1935 (AMNH 99484, -91).

Borneo. Baram, Sarawak: 1 ad. ♂, 1 juv. ♀, alc., skulls, C. Hose (BMNH 1907.29.2-3). Longison Island, East Coast British North Borneo: 3 ad. ♂♂, 3 ad. ♀♀, alc., 24-VI-1931 (ZRCS 7190-95). Kubonatok Cave, Dallas, Lahad Datu, East Coast Borneo: 2 ad. ♂♂, 1 ad. ♀, 2 subad. ♀♀, skins, P. Orolfo, 24-IX-1930 (ZRCS 7182-86). Perboewa (Landak), 900 m: 1 ad. ♀, skin, skull, J. J. Menden, 17-VIII-1937 (AMNH 106831). Burma. Tagoot, Gt. Tenasserim river: 1 ad. ♀, skin, G. C. Shorridge, 19/20-IV-1914 (HZM 3.1851), and 1 ad. ♀, skin, skull, same collector, 19-IV-1914 (ZRCS 795/16).

Celebes. Gorontalo: 1 ad. ♂, alc., skull, 1 ad. ♂, skin, skull, A. B. Meyer (ZMB 4203, 5389). Talassa (Maros), 300 m: 7 ad. ♂♂, 2 ad. ♀♀, skins, skulls, Heinrich-Expedition, XI-1933 (AMNH 153566-68, -70, -71, -72, -74, -75, -77). Enggano. Boeah-Boeah, ± 100 m: 2 ad. ♂♂, 1 ad. ♀, skins, skulls, de Jong, 5-VII-1936 (MZB 305-307/36); 1 ad. ♀, alc., skull, Modigliani (BMNH 1894.1.7.2).

Flores. "Flores": 1 ad. ♂, skin, skull, A. R. Wallace (holotype of *Eleutherura infumata* Gray, 1870; BMNH 1863.12.26.12). Borong, 50 m: 1 ad. ♂, skin, skull, J. Verheyen, 31-III-1971 (RMNH 28254). Waé-Ntjuang, Wankung, Rahong, 900 m: 1 ad. ♀, skin, skull, J. Verheyen, 25-V-1971 (RMNH 28255).

Japen Island. Seroei, Geelvinkbaai: 1 ad. ♂, skin, skull, G. Stein, 28-III-1931 (holotype of *Rousettus stresemanni* Stein, 1933; ZMB 44528). 1 mile N.W. Samberbaba: 1 ad. ♂, skin, skull, L. P. Richards, 29-X-1962 (AMNH 160264).

Java. "Java": 1 ad. ♂, alc., skull, H. A. Bernstein, Zoologisches Museum Breslau (ZMB 34132).

- Buitenzorg (= Bogor): 1 juv. ♂, alc., skull, M. Weber no. 607, 1888 (ZMA 16.676). Kp. Pautjasan, near Buitenzorg: 1 subad. ♀, skin, damaged skull, Saan, 21-VIII-1938 (MZB 115/38). Bolang, west of Buitenzorg: 3 ad. ♂♂, 3 ad. ♀♀, 1 juv. ♀, skins, skulls, H. J. V. Sody, 5-IX-1928 (RMNH 28256-59, -63, -64, -66); 1 ad. ♀, 1 ad. ♂, alc., skull H. J. V. Sody (ZMB 40862-3). Cave Tjineam, Preanger: 1 ad. ♂, 1 ad. ♀, skins, skulls, F. Kopstein, III-1928 (MZB 1517-8). Goeha Lalaj near Tjineam, Preanger: 1 ad. ♂, 6 ad. ♀♀, skins, skulls, F. Kopstein, III-1928 (MZB 163/39, 165-, 167-, 168-, 169-, 171-, 172/39). Tasikmalaja: 3 ad. ♀♀, skins, skulls, H. J. V. Sody, IV-1928 (RMNH 28260-62). Cave S.E. of Tasikmalaja: 2 ad. ♀♀, 1 subad. ♀, skins, skulls, F. Kopstein & W. C. van Heurn, IV-1928 (RMNH 2909-11).
- ?Java. (No locality on label): 4 ad. ♂♂, 1 juv. ♂, 1 ad. ♀, 2 subad. ♀♀, 1 juv. ♀, skins, skulls, M. Bartels (?1935) (RMNH 14929-37; 14929 has "Pn.", 14937 "Po." as locality); 2 ad. (sex?), skins, skulls, H. J. V. Sody (RMNH 28272-73).
- Kisar Island. "Kisser": 1 ad. ♂, alc., skull (ZMB), 2 ad. ♀♀, alc. (ZMB), 2 ad. ♀♀, skulls (ZMB 66520-21), 1 subad. ♀, skin (ZMB), H. Rolle, 11-XI-1901.
- Krakatau. Krakatau Island: 2 juv. ♂♂, alc., G. Lincoln (BMNH 74235-36). Long Island: 2 ad. ♂♂, 2 ad. ♀♀, skins, skulls, K. W. Dammerman, XII-1933 (ZMB 3377-80).
- Malaya. Bt. Lanjan, Damansara, Selangor: 1 ad. ♂, alc. (skull not extracted) (IMR R87.851). Bt. Lanjan, Sg. Buloh F. R., Selangor: 1 ad. ♀, alc. (skull not extracted) (IMR R94.014). Bukit Lagong forest reserve, Kepong, Selangor: 1 subad. ♂, 1 juv. ♂, alc., 1954, 1949 (BMNH 60609-10). Batu Caves, Selangor: 1 ad. ♂, skin, skull, 1903 (HZM 1.1660); 1 ad. ♂, alc. (ZRCS 7187), 1 ad. ♀, skin, skull, Survey Vert. Fauna Malay Peninsula, XII-1903 (ZRCS 918/11), 1 ad. (sex?), skull (ZRCS 909/11). "Perak": 1 subad. ♀, alc., skull, E. Hartert (ZMB 10222). Sua Betong estate, Port Dickson, Negeri Sembilan: 1 ad. ♀, skin, skull, G. Thompson, 21-VI-1975 (HZM 4.8155). "Purchased in Lima, Malaya": 1 ad. ♂, skull, via Zoological Society of London (BMNH).
- Mentawai. North Pagai (= Utara Island): 1 ad. ♂, skin, skull, J. J. Menden, 12-I-1935 (AMNH 103320).
- Muna. Raha: 1 subad. ♂, skin, skull, H. J. V. Sody, 1940 (RMNH 28265).
- Ndao Island. Pulau Dao, 30 m: 2 ad. ♂♂, 1 juv. ♂, 1 ad. ♀, skins, skulls, J. Verheyen, 16/19-IV-1969 (RMNH 28250-53).
- New Guinea. Moanouna, S.E. Milne Bay, 50 m: 1 ad. ♂, skin, skull, R. F. Peterson, 3-XII-1956 (AMNH 159030). Dabora, Tapitapipi caves, Cape Vogel peninsula, 65 m: 1 ad. ♀, skin, skull, H. M. van Deusen, 16-IV-1953 (AMNH 157289). Bena Bena river, 8 miles S.E. of Goroka, East High District, ca. 4700 ft.: 1 ad. ♂, skin, skull, H. M. van Deusen, 22-VIII-1959 (AMNH 191211). Madang, Madang District: 6 ad. ♂♂, 7 ad. ♀♀, skulls, J. C. Hafner, 22-VII-1969 (MVZ 141113-22, -24, -25, -26). Maiwara, 10 miles North of Madang, Madang District: 18 ad. ♀♀, skulls, W. R. Johnson, 26-VI to 2-VIII-1969 (MVZ 140172-84, -88, -92); 1 ad. ♀, skull, L. E. Green, 25-VII-1969 (MVZ 140172); 1 ad. ♀, skull, J. C. Hafner, 20-VII-1969 (MVZ 141110). Admosin Island, 3/4 mile N.W. Alexishafen, Madang District: 1 ad. ♀, skull, W. R. Johnson, 21-VI-1969 (MVZ 140163). Raut, 1750 ft.: 1 ad. ♂, alc., Aberdeen Univ. Exploration Soc. Expedition, 27-VII-1973 (BMNH). Hollandia (= Jayapura): 1 juv. ♂, skin, skull, F. Hoekzema, III-1956 (ZMA 2692). Noordwijk, Hollandia: 1 ad. ♀, alc., F. Hoekzema, 19-V-1959 (ZMA 2693). Cycloop Mt., 150 m: 1 ad. ♀, skin, skull, New Guinea Expedition, 30-IV-1939 (AMNH 152446). Mt. Arfak: 1 ad. ♂, skin, skull, Bruyn (ZMB 10255). See also Bagabag Island and Japen Island.
- Nusa Penida: 3 ad. ♂♂, 4 ad. ♀♀, skins, skulls, V. v. Plessen, 27-II-1938 (MZB 121-22/38; ZMB 90509; AMNH 107650-52, -54).
- Peleng Island: 1 ad. ♂, 1 ad. ♀, skins, skulls, J. J. Menden, 23-VII-1938 (MZB 189-90/38); 1 ad. ♂, 1 subad. ♂, 2 ad. ♀♀, 1 subad. ♀, skins, skulls, J. J. Menden, 30-VI/23-VII-1938 (AMNH 109045-46, -48, -53, -54).

- Philippines. Balabac Island. "Balabac": 1 ad. ♂, 1 subad. ♀, skins, skulls, J. Ramos, 1/3-II-1963 (AMNH 207585-86). Minagas Point, Dalawan Bay: 1 ad. ♀, skin, damaged skull, M. C. Thompson & R. Gonzales, 24-IV-1962 (USNM 477537).
- Busuanga Island. 6 km N.E. San Nicolas: 2 ad. ♀♀, skins, skulls, M. C. Thompson, 24/27-V-1962 (USNM 477539-40).
- Cebu Island. "Cebu": 1 juv. (sex?), alc., skull, A. Krapfenbauer, 7-VIII-1901 (ZMB 54027). Corte, Danao City: 1 ad. ♂, skin, skull, D. S. Rabor, 16-V-1963 (AMNH 207484). Guinano-ran, Cebu City: 1 ad. ♀, skin, skull, D. S. Rabor, 15-X-1962 (AMNH 207490). Tisa, Cebu City: 3 subad. ♂♂, 1 ad. ♀, 2 subad. ♀♀, skins, skulls, D. S. Rabor, 23-X-1961, 15-VIII- and 21-XII-1962 (AMNH 207483, -89, -93 to -96).
- Leyte Island. Abuyog, Bo. Balinsasayao: 1 subad. ♂, skin, skull, American Philippine Expedition (AMNH 187863).
- Luzon Island. Manilla: 1 ad. ♂, skin, skull (holotype of *Eleutherura philippinensis* Gray, 1870; BMNH 1858.3.29.1). "Luzon": 1 ad. ♂, 1 ad. ♀, alc., Grace T. Seton Far East Collection, XII-1930 (FMNH 34660-61).
- Montalban: 1 ad. ♂, alc., skull, Paul Bartsch, 5-VII-1908 (USNM 175845). San Mariano, Sierra Madre Mts., Isabella Prov., 750 ft.: 5 ad. ♂♂, 5 ad. ♀♀, skins, skulls, American Philippine Expedition, 25-IV-1961 (AMNH 187092, -93, -95, -97 to -99, -101, -104, -105, -109). Benguet, 5000 ft.: 1 subad. ♂, skin, skull, 14-II-1894 (BMNH 1897.5.2.5); 1 ad. ♀, skin, skull, G. Whitehead, 14-II-1894 (BMNH 1897.5.2.6). Jamtik: 1 ad. ♀, alc., skull; 1 ad. ♀, 1 subad. ♀, alc.; 1 ad. (sex?), skull, Jagor (ZMB 10194-97).
- Mindanao. Initao: 1 ad. ♂, 1 ad. ♀, 1 subad. ♀, skins, skulls, S. Daan & N. K. Bierma, 4-III-1971 (ZMA 14.412-14). Luangbay cave, Sitio Tegato, Davao: 1 ad. ♂, 1 ad. ♀, skins, skulls; 4 ad. ♂♂, 1 subad. ♂, alc., skulls; 2 ad. ♀♀, 6 subad. ♀♀, alc., American Philippine Expedition, 22-X-1946 (FMNH 61353-55, -59, -61, -66 to -72, -83, -85). Tawang cave, Samal Island, Davao gulf, sea level: 2 ad. ♂♂, 1 ad. ♀, 1 subad. ♀, skins, skulls, American Philippine Expedition, 1/2-XII-1946 (FMNH 56443-46).
- Negros. "Negros": 2 subad. (sex?), skulls, J. B. Steere, II-1888 (USNM 105223-24); 1 juv. ♂, alc. (USNM 254467). Siaton, Negros Oriental: 4 ad. ♂♂, alc., D. S. Rabor, 8-VIII-1952 (FMNH 80471-74).
- Palawan. Macagua, Brooke's Point: 1 ad. ♀, 1 subad. ♀, skins, skulls, D. S. Rabor, 4-IV-1962 (USNM 477533-34).
- Polillo. "Polillo": 1 ad. ♀, skull, E. H. Taylor, VII-1920 (AMNH 241711; skin measurements published by Taylor 1934: 175).
- Samar. "Samar": 2 ad. ♀♀, alc. (ZMB 10198). Borragan, 1 ad. ♂, alc., skull, Jagor (ZMB 2524).
- Roti. "Rotti": 1 ad. ♂, skin, A. Bühler, IX-1935 (NHMB A4918); 1 ad. ♂, 1 subad. ♀, skins, A. Bühler & W. Meyer, 1936 (NHMB A4919-20).
- Sawu. "Savu": 1 subad. ♀, alc., skull, A. Everett, VIII-1896 (BMNH 1897.4.8.10); 1 subad. ♀, skin, skull (BMNH 1908.7.26.7).
- Solomon Islands. Bougainville. Mamalomino, Buin Distr.: 1 subad. ♂, skin (probable holotype of *Rousettus amplexicaudatus hedigeri* Pohle, 1952; ZMB). Base of Mt. Balbi, Togarau, Wankunai, ± 600 m: 1 ad. ♂, 1 ad. ♀, skins, skulls, A. B. Mirza, 6/8-IV-1968 (BBM NG61328, -46). Mutahi, Bougainville Distr., 700 m: 1 ad. ♀, skin, skull, 23-III-1968 (BBM NG61307).
- Choiseul. Malangona, ± 10 m: 2 ad. ♂♂, 1 ad. ♀, alc., skulls, P. Temple, 11/18-III-1964 (BBM BSIP23642, -58, -93).
- Fauro. Toumoa, ± 10 m: 1 ad. ♀, alc., skull, P. Temple, 12-IV-1964 (BBM BSIP23804).
- Guadalcanal. "Guadalcanal": 2 ad. ♂♂, 5 ad. ♀♀, 1 subad. ♀, alc., E. Paravicini, 1929 (NHMB 4150-57). Tabalia: 1 ad. ♂, alc., skull, P. J. Shanahan, 29-V-1964 (BBM BSIP23915).
- Kolombangara. Pepele, ± 10 m: 2 ad. ♂♂, alc., skulls, P. Temple, 6/10-II-1964 (BBM BSIP23472, -501).
- Malaita. Dala, ± 20 m: 1 subad. ♀, alc., skull, P. J. Shanahan, 29-VI-1964 (BBM BSIP-24079).
- Vella Lavella. "Vella Lavella", ± 10 m: 1 ad. ♀, alc., skull, P. Temple, 9-XII-1963 (BBM BSIP23274). Ulo Crater, ± 10 m: 1 ad. ♀, alc.,

- skull, P. Temple, 13-XII-1963 (BBM BSIP-23302).
- S. Ysabel. Tatamba, ± 20 m: 3 ad. ♂♂, 1 subad. ♂, 3 ad. ♀♀, skins, skulls, P. Shananan, 31-VIII/1-IX-1964 (BBM BSIP24309, -11, -12, -15, -16, -19, -35). Talise, San Jorge Island: 1 ad. ♂, alc., J. Grant, 23-XI-1965 (BMNH 67.19.18).
- Sumatra. "Sumatra": 1 ad. ♀, skin, skull, J. Turner (BMNH 1938.3.13.36); 1 subad. (sex?), skeleton, skull (RMNH; Jentink, 1887: 263, specimen d). Kalianda, 100 m: 1 ad. ♂, skin, skull, J. J. Menden, 2-VIII-1934 (AMNH 102917).
- Sumba. Melolo: 1 ad. ♂, skin, skull, G. Stein, 17-VI-1932 (ZMB 92148); 1 ad. ♂, alc., A. Bühler & E. Sutter, 2-VI-1949 (NHMB A5659). Mao Marros: 1 subad. ♂, skin, skull, G. Stein, 8-VI-1932 (ZMB 92147). Near Matawai Kenor near Prai Jawang: 1 ad. ♂, 1 juv. ♂, 4 subad. ♀♀, alc. (skulls extracted, but not examined), A. Bühler & E. Sutter, 13-VI-1949 (NHMB A5660-65); 1 subad. ♀ without data in same bottle as preceding (NHMB).
- Talisai. Cave, Talisse: 1 ad. ♂, 2 subad. ♀♀, skins, skulls, Klapperproefstation Manado, VIII-1933 (MZB 21-23/34).
- Thailand. Bangkok: 1 ad. ♀, alc., skull, v. Martens (ZMB 3238). Chiangmai, North Siam: 1 ad. ♂, alc., H. G. Deignan, 10-XII-1931 (ZRCS 7189). Doi Pahompok, Fang Distr., Chieng Mai, 6800 ft.: 1 juv. ♂, skin, skull, S. Pantuwatana, 4-XI-1965 (BMNH 70-1351). Pok Nam Tok, 21 km from Saraburi: 1 subad. ♀, 1 ad. ♀, skins, skulls, Somchai Imlarp, 19-I-1965 (BMNH 70.1351A, 70.1352).
- Timor. Nikiniki, 750 m: 3 ad. ♂♂, 4 ad. ♀♀, 1 subad. ♀, skins, skulls: 1 subad. ♂, skin, G. Stein, 27/30-III-1932 (MZB 209/35, 211-14/34, ZMB 51241-42, 92082-84); 1 ad. ♂, 2 ad. ♀♀, skins, skulls, Mrs. Walsh, III/IV-1929 (MZB 2209-11); 1 ad. ♂, 3 ad. ♀♀, 6 subad. ♀♀, alc., A. Bühler, VI-1935 (NHMB A4892-901). Dili: 2 ad. ♂♂, 2 ad. ♀♀, skins, skulls, R. E. Goodwin, 7-III, 6-IV, 10-V-1968 (AMNH 237608, -21, -37, -39). Soë: 1 ad. ♂, alc., A. Bühler, VI-1935 (NHMB A4891).
- Rousettus celebensis* Andersen, 1907
- Celebes. Kuala Navusu, near Parigi: 1 ad. ♂, skin, skull, C. P. Groves, XI-1975 (ZMA 18.571). Gorontalo: 1 ad. ♀, skin, skull, A. B. Meyer (ZMB 5390). Main, Minahassa: 2 ad. ♂♂, 1 ad. ♀, skins, Cursham, 1-III-1894 (ZMB 92351, -52, -54). Minahassa: 1 subad. (sex?), skull, Dr. Warburg, 1891 (ZMB — Hamburg 22053). Makassar: 6 ad. ♂♂, 9 ad. ♀♀, skins, skulls, 1 ad. ♂, skin, 2 ad. ♂♂, skulls, G. Stein, 21/23-I-1931 (ZMB 91787-800, 51235-38). Api: 1 ad. ♀, skin, skull, Cursham, 22-VIII-1894 (ZMB 92353). Tangkopo, Batuangus, near Bitung: 4 ad. ♀♀, heads and one skin, alc., C. & D. Jones (BMNH 78.964-67).
- Sangihe Islands. Sangihe. "Gross Sangi": 1 ad. ♂, skin, A. B. Meyer, 27-VII-1893 (RMNH 12765); 1 ad. ♂, skin, Cursham (ZMB 92347). Siau Island. "Siau": 2 ad. ♀♀, 1 ad. (sex?), skins, skulls, Cursham (ZMB 92348-50); 1 ad. (sex?), skull, Meyer (ZMB 2169); 1 ad. ♀, skin, A. B. Meyer, 17-VII-1894 (RMNH 12764).
- Tahulandang Island. "Tagulandang": 2 ad. ♀♀, skins, skulls, 1 ad. ♀, skin, Cursham, 4/8-VIII-1894 (ZMB 92355, -56, -58).
- "Celebes oder Talautinseln oder Sangirinseln": 1 ad. ♀, skin, skull, Cursham (ZMB 92357).
- Rousettus leschenaultii leschenaultii* (Desmarest, 1820)
- Burma. "Burma": 1 ad. ♂, alc., skull, Day (ZMB 3949). Moulmein caves: 2 ad. ♂♂, 1 ad. ♀, alc., skulls, J. Armstrong, 1877 (ZSI 18702-04). Yado-Casin hills, Alta Birmania: 2 ad. ♀♀, alc., L. Fea, II-1888 (MSNG CE44552).
- Cambodia. Angkor Vat: 2 ad. ♂♂, 1 ad. ♀, alc., Dr Harmand, 1877 (MNHN CG1979-382-4) (identification with reservation).
- China. Kanton, Kuang tung (= Kwantung Prov.): 1 ad. ♂, 1 ad. ♀, skins, skulls, R. Mell, captured VII-1917, died 16-XI-1917 (ZMB 43252-3). Wutsung, Kuang tung: 1 ad. ♂, 1 subad. ♂, alc., skulls, 1 ad. ♂, skin, 1 ad. ♀, skin, skull, R. Mell, 5-VI-1914 (ZMB 43257-60).
- Hong Kong. "Hong Kong": 1 ad. ♂, skin, skull, Schoenlein, 1846 (ZMB 352).

India. "India": 1 ad ♀, alc., Gerrard, London (MSNG CE46651); 1 subad. ♀, alc., M. Dussumier (MNHN, possibly CG1835-81). Bengal: 1 ad. ♀, skin, skull, Lamare Piquot (ZMB 3441). Bhubaneswar, Orissa: 1 ad. ♀, skin, skull, 12-II-1967, G. Topál (MNM). Calcutta: 1 subad. ♀, alc., skull (holotype of *Cynonycteris infuscata* Peters, 1873; ZMB 361). Madras: 1 ad. ♂, alc., Mitchell (ZMB 3956). Khaneri Caves, near Bombay: 1 ad. ♂, 1 ad. ♀, skins, skulls, 9-VII-1967, G. Topál (MNM). Koira, Sundargarh Distr., Orissa: 1 ad. ♂, 1 subad. ♂, 3 ad. ♀♀, alc., skulls, P. K. Das, 11/14-VII-1973 (ZMA 20492-94, -96, -97). Kanchanpur, Rest House, Tripura: 1 ad. ♂, alc., skull, V. C. Agrawal, 12-II-1971 (ZSI 19426). Poona, Parvati Cave: 3 ad. ♂♂, 9 ad. ♀♀, skins, skulls, 5-VIII-1967, G. Topál (MNM). Sei Josa, Kameng (Frontier Division), Arunachal: 1 ad. ♂, alc., skull, 1 ad. ♀, 2 juv. ♀♀, alc., V. C. Agrawal, 18-VII-1977 (ZSI).

Thailand. Ban Na Sao, South Siam: 1 ad. ♀, alc., skull, 1920 (ZRCS 7218).

Vietnam. "Saigon?": 1 juv. (sex?), alc., Dr Harmand, 1877 (MNHN CG1877-620). Hué: 1 ad. ♂, skin, F. Lataste (BMNH 19.7.7.2470).

Rousettus leschenaultii shortridgei Thomas & Wroughton, 1909

?Aru. "Aru": 1 ad. ♂, alc., skull, Gerrard (ZMB 4412).

Bali. Oeboed: 9 ad. ♂♂, 7 ad. ♀♀, 1 subad. ♀, 2 juv. ♀♀, skins, skulls, V. v. Plessen, 27-XII-1937 to 7-I-1938 (ZMB 92010-16, 90407-16, 90415 "b", 90420). Selat: 2 subad. ♀♀, skins, skulls, V. v. Plessen, 4-I-1938 (ZMB 90417-18).

Java. Buitenzorg (= Bogor): 1 ad. ♂, alc., skull, M. Weber no. 610, 1888 (ZMA 16.656); 1 ad. ♂, skin, skull, W. C. van Heurn, 26-II-1920 (RMNH 28238); 5 ad. ♀♀, skins, skulls, W. C. van Heurn, VIII-1919, II/III-1920 (RMNH 28239-43). Kp. Pantjasan, near Buitenzorg: 1 ad. ♀, skin, skull, Saan, 21-VIII-1938 (MZB 116/38). Cheribon (= Ceribon): 1 ad. ♂, skin, skull, J. J. Menden, 2-X-1932 (ZMB 39606); 1 subad. ♀, skin, skull, J. J. Menden, 13-VI-1937 (ZMB 48612). Cave Tjikareo, Tjineam, Preanger: 2 ad. ♀♀, skins, skulls, F. Kopstein, V-

1928 (MZB 1768-69). Toeloengagoeng, Kediri: 1 ad. ♀, skin, skull, C. J. Louwerens, V-1937 (MZB 101/37). Tjandi Paree, Porrong Distr., Soerabaya: 33 ad. ♀♀, 1 subad. ♀, skulls, J. H. F. Kohlbrugge (ZMU 300).

"West Java": 1 ad. ♀, alc., skull, J. F. van Bemelen (RMNH 28040). Tjiparaj, Soekaboemi: 1 ad. ♂, 2 ad. ♀♀, skins, skulls, Max Bartels, 1940 (MZB 596-98/40). Tjandi, Wijnkoopsbaai: 1 ad. ♂, 2 ad. ♀♀, skins, skulls, P. F. Franck, 27-IV-1940 (MZB 209-11/40). Cave near Palaboehan Ratoe (= Wijnkoopsbaai): 5 ad. ♂♂, 1 ad. ♀, 1 subad. ♀, 3 juv. ♀♀, skins, skulls, V. v. Plessen, 30-I-1935 (ZMB 48743-46, 49379-84).

Sumatra. Kalianda, 100 m: 1 ad. ♂, skin, skull, J. J. Menden, 2-VIII-1934 (ZMB 39608). Sinabang, Simalur (= Simeuluë Island): 1 ad. ♂, alc., skull, E. Jacobson (RMNH 28042, alc. no. 1744).

Rousettus spinalatus Bergmans & Hill, 1980

Borneo. Niah Great Cave, Sarawak: 1 subad. ♀, skin, skull, T. Harrison, 6-XI-1965 (BMNH 75.589). Ulu S. Pandan, Bintulu, Sarawak: 1 ad. ♀, alc., skull, E. Banks, 1932 (ZRCS 7188).

Sumatra. Northern Sumatra (either in or near Medan, or in or near Prapat): 1 ad. ♀, skin, skull, and 1 juv. ♂, alc., collected by natives for Dr Kern, XII-1977 (holotype and paratype of *Rousettus spinalatus* Bergmans & Hill, 1980; NMW 24112-3).

METHODS

Of all specimens examined by the first author, the following body and skull measurements were taken (with callipers, to the nearest 0.1 mm):

forearm length — taken in situ, including joints with upper arm and hand (with upper arm and metacarpals pressed against forearm as closely as possible, without forcing);

lengths of all metacarpals and 1st phalanges, and lengths of 2nd phalanges of 3rd, 4th and 5th digits — measured in situ (not stretched), from end or tip to middle of joint, or between middles of joints;

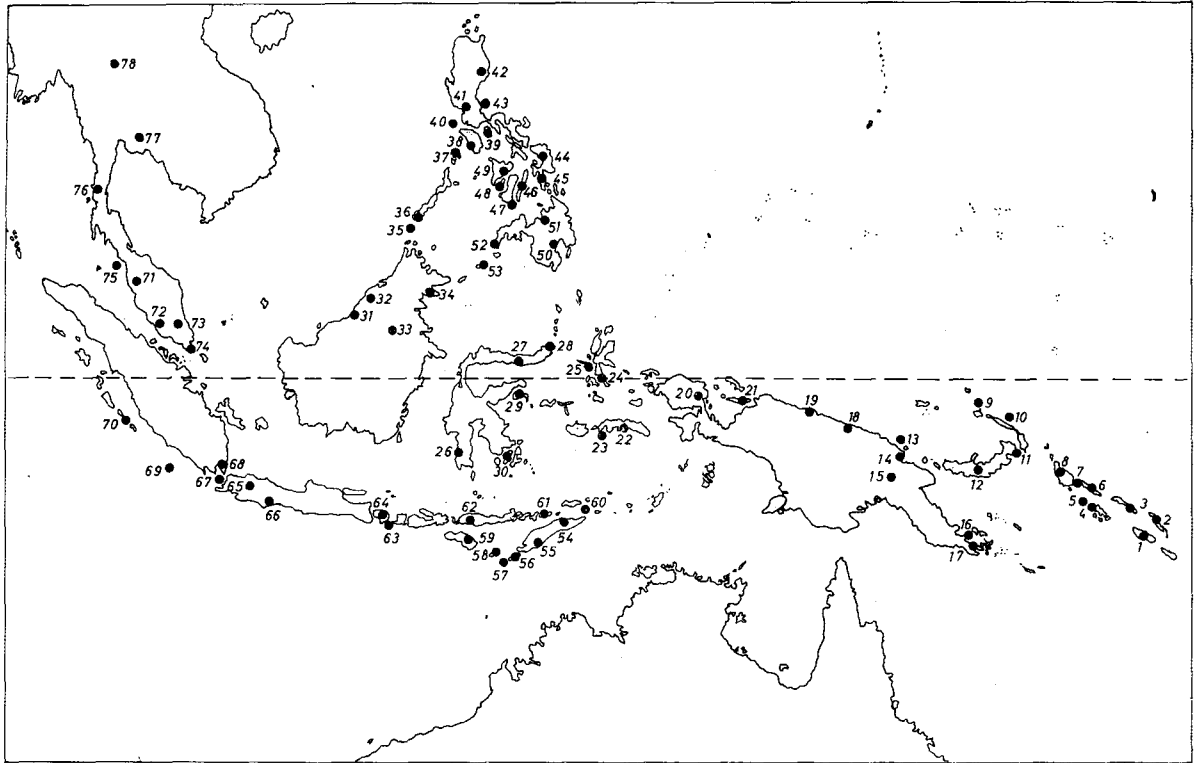


Fig. 1. Distribution of *Rousettus amplexicaudatus*. Localities taken from labels of museum specimens (specified in the section on Material examined), and from the literature as cited. (Localities not found on map: New Guinea: Kiowa Rock shelter, Chimbu prov. (Menzies 1977: 335); Philippines: Benguet and Jantik; Abra Province, Luzon (Lawrence 1939: 34); Thailand: Ban Na Sao.) 1. Guadalcanal: Tabalia. 2. Malaita: Dala. 3. Santa Ysabel: Tatamba; Talise on S. Jorge Island. 4. Kolombangara: Pepele. 5. Vella Lavella: Ulo Crater. 6. Choiseul: Malangona. 7. Fauru: Toumoa. 8. Bougainville: Mamalomimo, Mt. Balbi, Wakunai; Mutahi, Bougainville District. 9. Emira Island. 10. Tabar Island. 11. Duke of York Island. 12. New Britain: Kandrian. 13. Bagabag Island. 14. New Guinea: Madang; Maiwara, north of Madang; Admosin Island, 3/4 mile N.W. of Alexishafen. 15. New Guinea: Bena Bena river, S.E. of Goroka; Bulolo (Lidicker & Ziegler 1968: 28); Ihu (McKean 1972: 3). 16. New Guinea: Dabora, Cape Vogel peninsula. 17. New Guinea: Moanouna, S.E. Milne Bay. 18. New Guinea: Rautit. 19. New Guinea: Jayapura (= Hollandia); Noordwijk near Jayapura; Cyclop Mt. 20. New Guinea: Mt. Arfak. 21. Japen Island: Serui, 1 mile N.W. Samberbaba. 22. Ceram (Jentink 1888: 151). 23. Ambon. 24. Halmahera: Patani (Dollman 1930: 431). 25. Ternate (Jentink 1887: 263). 26. Celebes: Talassa near Maros. 27. Celebes: Gorontalo. 28. Talisai Island. 29. Peleng Island. 30. Muna Island: Raha. 31. Sarawak: Niah caves (Medway 1977: 57-58). 32. Sarawak: Baram. 33. Kalimantan: Perboewa (Landak river). 34. Sabah: Madai cave near Lahat Datu (Chasen 1931: 110); Kubonatak cave, Lahad Datu; Longison Island. 35. Balabac Island: Minagras Point. 36. Palawan: Macagua, Brookes Point. 37. Busuanga: 6 km N.E. San Nicolas. 38. Mindoro: Mamburao (Lawrence 1939: 34). 39. Mindoro: Calapan (Lawrence 1939: 34). 40. Lubang (Hollister 1913: 305; Lawrence 1939: 34). 41. Luzon: Manilla; Montalban. 42. Luzon: San Mariano, Sierra Madre Mts. 43. Polillo. 44. Samar: Borragan. 45. Leyte: Abuyog. 46. Cebu: Corte, Danao City; Guinanoram and Tisa, Cebu City; Kawit near Bogo (Lawrence 1939: 34). 47. Negros: Siaton; P. Dumaguete; Himamaylan (Sanborn 1952: 98). 48. Guimaras (Hollister 1912: 9). 49. Panay: South East (map in Taylor 1934: 173). 50. Mindanao: Sitio Tegato, Davao; Samal Island; Misamis district (Lawrence 1939: 34); Madaum, near Davao (Sanborn 1952: 98). 51. Mindanao: Initao. 52. Mindanao: Zomboanga (Lawrence 1939: 34). 53. Jolo Island (Taylor 1934: 172). 54. Timor: Dili; Beciã, Ossu; Metinaro; Atsabe (cf. Goodwin 1979: 84). 55. Timor: Nikiniki; Soë. 56. Roti. 57. Ndao Island. 58. Sawu. 59. Sumba: Melolo; near Prai Jawong. 60. Kisar Island. 61. Alor. 62. Flores: Borong; Waë-Ntjuang, Rahong. 63. Nusa Penida. 64. Bali: Ubud; Selat; Soka. 65. Java: Bogor; Kp. Pantjasan near Bogor; Bolang, west of Bogor. 66. Java: Tasikmalaja; cave S.E. of Tasikmalaja; Tjineam (Preanger); Goeha Lalaj near Tjineam; Kaliputjang, Tji-Tandoei river (Preanger). 67. Krakatau: Lang Island (= P. Rakata ketjil). 68. Sumatra: Kalianda. 69. Enggano: Boeah-Boeah. 70. Mentawai Islands: Pagai Utara. 71. Malaya: Perak. 72. Malaya: Bt. Lanjan, Damansara (Selangor); Bt. La-gong forest reserve, Kapong (Selangor); Batu caves (Selangor); Port Dickson (Negeri Sembilan). 73. Malaya: G. Brinchang, Pahang (Medway 1969: 10). 74. Singapore (Harrison 1974: 96). 75. Langkawi Island (Medway 1969: 10). 76. Burma: Tagoot, Gt. Tenasserim river. 77. Thailand: Bangkok (= Krung Thep); Pok Nam Tok, near Saraburi. 78. Thailand: Doi Pahompok, Chieng Mai district; Chieng Mai. Fecit J. Zaagman.

other body measurements, such as total length, tail length, ear length and foot length — copied from the labels whenever available;

greatest skull length — between prosthion and opisthocranion, the latter situated either on occipital region of braincase, or in median plane on line connecting most caudal points of condyli occipitales, or on sagittal/occipital crest;

condylobasal length — between prosthion and intersection of median plane and line connecting most caudal points of condyli occipitales;

rostrum length — between prosthion and most anterior (or distal) point of orbit margin;

palatal length — between prosthion and intersection of tangent of middle of caudal margin of palatum and median plane;

cranium width — between most distal points of braincase above posterior zygomatic arch insertions;

interorbital width — between innermost points of interorbital constriction of skull roof;

postorbital width — between innermost points of postorbital constriction of skull roof;

zygomatic width — between most distal points of zygomatic arches;

mandible length — between most distal point of mandibulum and most posterior point of a condylus articularis;

mandible height — shortest distance between tangent plane of ventral side of mandibulum and most dorsal point of processus coronoideus;

teeth row lengths, widths over canines and molars, and lengths and widths of individual teeth — over cingula; teeth lengths in line with orientation of teeth row, teeth widths perpendicular to their lengths.

Of the specimens measured by Bergmans and Glas (see page 3), no body measurements other than forearm lengths were taken, and but some important skull (and teeth: Bergmans) measurements, with callipers. Of the specimens measured by Hill (see page 3) only forearm lengths and some important skull measurements (condylobasal length, rostrum length, zygomatic width, and cranium width) were taken (with the exception of the holotype specimen of *Eleutherura infumata* Gray, which was measured more in detail) — on our request.

Specimens with closed sutures between basioccipital and sphenoid and between sphenoid and vomer have been considered as full-grown adults. The tables include only measurements of such specimens.

In measurements, males always average larger than females (compare Phillips, 1968); therefore the sexes have been treated separately. The designation of teeth is after Andersen.

The synonymies are restricted to the literature since Andersen, 1912, but only in the case of *R. amplexicaudatus* we have aimed at completeness. Pre-1912 references can usually be retrieved in the extensive synonymies provided by Andersen (1912). They are only repeated here if a new taxon is described, or if a locality is mentioned which can not be found in later publications. Known localities of *R. amplexicaudatus* are mapped (fig. 1). Notes on dental anomalies and ectoparasites are included in the Results.

RESULTS

Three subspecies of *Rousettus amplexicaudatus* are here distinguished: *amplexicaudatus* (Geoffroy, 1810), *infumatus* (Gray, 1870), and *brachyotis* (Dobson, 1877). As regards the other South-East Asian *Rousettus* species, our ideas are essentially in agreement with those of Andersen (1912). We recognize *R. leschenaultii*, with in the region concerned the subspecies *leschenaultii* (Desmarest, 1820) and *shortridgei* Thomas & Wroughton, 1909; *R. celebensis* Andersen, 1907; and *R. spinalatus* Bergmans & Hill, 1980.

Characters. — Andersen (1912) differentiated between the species of *Rousettus* of Southern and South-Eastern Asia mainly on the basis of size. This and other characters used by him and others are shortly reviewed in order to understand their reliability and usefulness.

Fur colour. According to Andersen (1912), *R. amplexicaudatus* is darker than *R. leschenaultii* (the subspecies *amplexicaudatus*, *minor* and *brachyotis* would have similar colours); and *R. celebensis* is brighter than *R. amplexicaudatus*. Possibly, therefore, colour can be used successfully to separate these three species (as *leschenaul-*

tii and *celebensis* are allopatric). Fur colour in *R. spinalatus* is rather as in *amplexicaudatus* but these species are readily distinguished anyhow. We consider it inopportune to attach much importance to the small differences in fur colours as observed in the presently studied and often old museum specimens.

Fur distribution. In distribution over the body, the furs of *amplexicaudatus*, *leschenaultii*, and *spinalatus* show no conspicuous differences (Andersen 1912; Bergmans & Hill, 1980). All three have an almost naked (and lighter coloured) neck region and an almost bare notopatagium. *R. celebensis* clearly differs. Its fur is longer and more woolly; the neck region is not clearly less hairy; and the notopatagium is for a large part covered with a dense fur. Adult specimens of both sexes (and not only in males, as Goodwin, 1979, claims) in all species but *spinalatus*, for which this is not yet known, may show two brightly coloured and bristly hairtufts in the lower neck region, one at either side. These occur especially in older specimens and are often absent, seemingly without any geographic regularity.

Body measurements. Differences in ear dimensions, tail length, and muzzle length were frequently used to distinguish *leschenaultii* from *amplexicaudatus* (see Dobson, 1876 and 1878b, and Andersen, 1912) and from *celebensis* (see Andersen, 1912). Museum skins do not allow these measurements to be taken with accuracy, and collector's measurements on labels have been taken in many different ways. For these reasons, we have not used them.

Wing measurements. Andersen (1912) used wing measurements only in his description of *celebensis*. For this study, bone lengths of 3rd, 4th and 5th fingers have been measured. Metacarpal lengths appeared to vary geographically and may serve to help determine the subspecific identity of certain specimens.

Baculum. Few bacula have been described: of *R. amplexicaudatus* from New Guinea (Krutzsch 1959) and from Bali and Celebes (Krutzsch 1962 figs. A-B), and one of *R. l. shortridgei* from Java (Krutzsch 1962 fig. C). Krutzsch considers these bones "similar in design". Agrawal & Sinha (1973) described the baculum of a typical *R. l.*

leschenaultii from Maharashtra, and two from Tripura and Burma belonging to "*R. a. amplexicaudatus*" (a debatable identification; see below). Possible morphological variation of the baculum is unknown and taxonomic use of the few published descriptions seems premature.

Skull shape. Dobson (1876; 1878b) does not mention skull characters at all. Andersen (1912) does not use them in his *Rousettus* key with regard to the species here considered, but refers to them in his descriptions. The rostrum in *amplexicaudatus* is "proportionally slenderer" than in *leschenaultii*; the orbits in *minor* (= *amplexicaudatus infumatus*) would perhaps be slightly larger than in *brachyotis*; the rostrum in *brachyotis* is "noticeably slenderer" than in *amplexicaudatus*; the palate in *celebensis* is narrower than in *brachyotis* (see Andersen, 1912). In an addendum Andersen (1912) added that *shortridgei* has a "relatively conspicuously broader rostrum and palate" than *leschenaultii*; and that the differences observed by him earlier between *amplexicaudatus*, *minor*, and *brachyotis* are in fact only expressions of different size ranges. According to Stein (1933) his *stresemanni* (here regarded as a synonym of typical *amplexicaudatus*) would answer the concept of the subgenus *Stenonycteris* Andersen, 1912 (erected solely for the East-African *Rousettus lanosus* Thomas, 1906), as it would possess the typically strong basicranial axis deflection. The skull of the type of *stresemanni*, however, does not differ in this respect from *amplexicaudatus* skulls, in which the alveolar line if projected backwards often passes through the upper part of the occipital condyles. (The deflection in *lanosus*, it may be observed, is more pronounced than in *amplexicaudatus* s.l.) The skull of *spinalatus* would hardly differ from that of *amplexicaudatus*; the more backward position of its M² might suggest a possibly relatively shorter rostrum, and its mandibular coronoid process may prove to be relatively high (Bergmans & Hill, 1980; this paper). Within *amplexicaudatus*, we could detect no appreciable differences in the shapes of skulls from different geographic regions.

Cranial measurements. Andersen (1912), in his *Rousettus* key, did not use skull size to discriminate between *leschenaultii*, *amplexicaudatus*, and/or

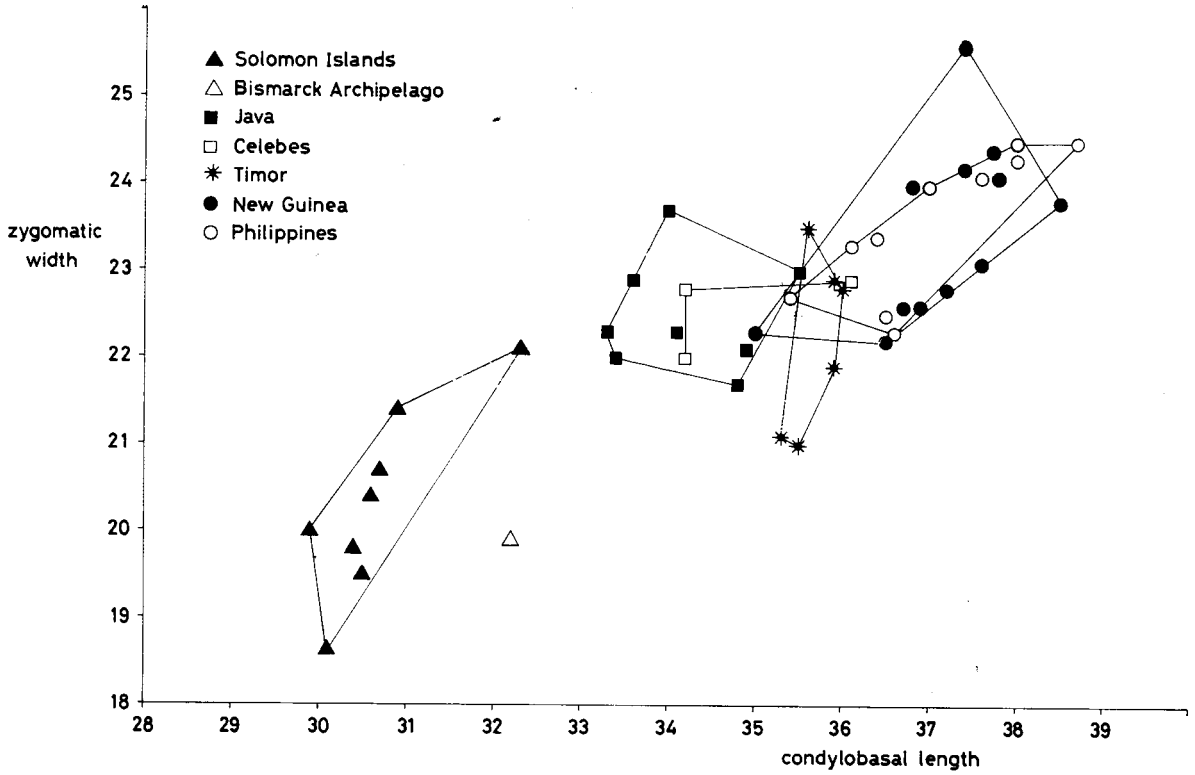


Fig. 2. The relation between condylobasal length and zygomatic width (both in mm) in males of some populations of *Roussetus amplexicaudatus*.

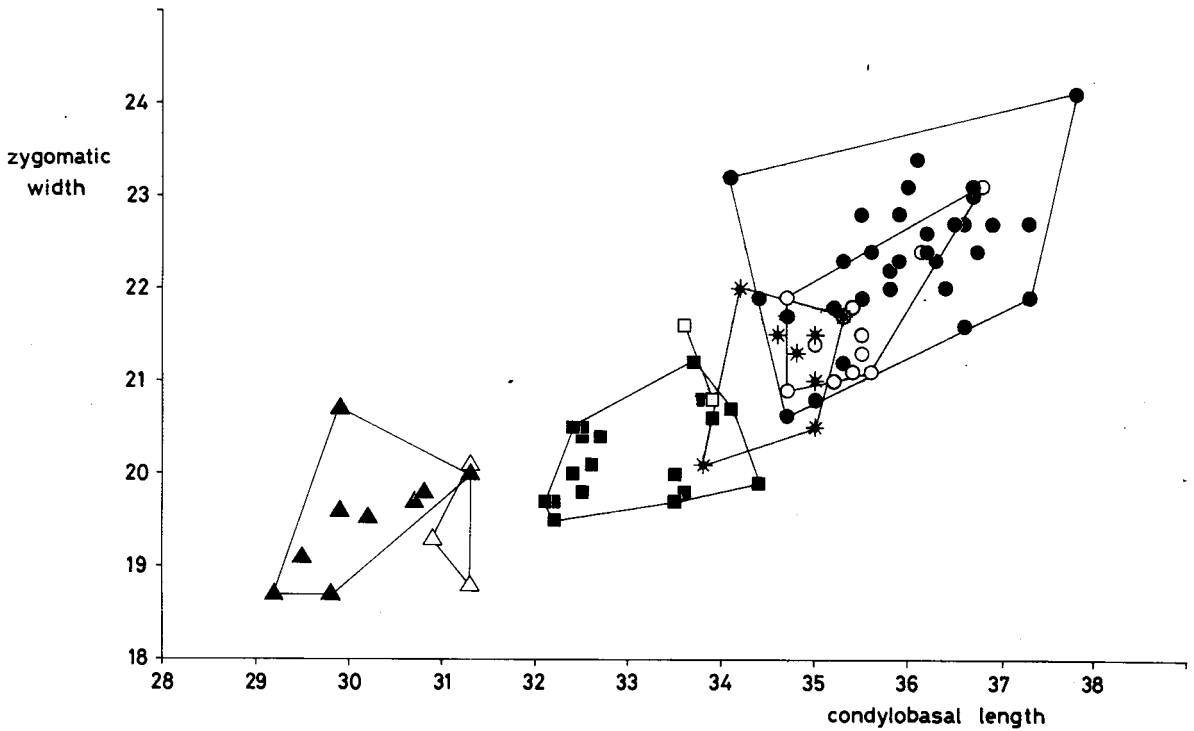


Fig. 3. The relation between condylobasal length and zygomatic width (both in mm) in females of some populations of *Roussetus amplexicaudatus*; symbols as in fig. 2.

celebensis. In his descriptions he stated that the skull of *amplexicaudatus* is "essentially as in *R. leschenaultii*, but averaging smaller", and of the skull of *celebensis* "General size as in *R. amplexicaudatus*". The skull size of *spinalatus*, as far as known, also falls in the same range (Bergmans & Hill, 1980; this paper). But within *amplexicaudatus* especially greatest skull length and condylobasal length provide the best means to distinguish between subspecies (or groups of populations). Skull width measurements tend to vary strongly within populations and, although averaging differently per subspecies, cannot be called diagnostic.

Dentition. Premolars and molars of *amplexicaudatus* vary in size. They are as large as in *leschenaultii* while their dimensions differ from those of *celebensis*. Andersen (1912) remarks that P¹ is deciduous in *brachyotis*; that P¹ in some cases is "closely wedged in" between C¹ and P³; and that the cheek-teeth are relatively crowded in *brachyotis*. While P¹ is in fact absent in a few specimens and the arrangement of the teeth is variable, these characters seem to vary individually rather than geographically (cf. Tate 1942). Bergmans & Hill (1980) list a number of slight but distinct morphological differences between dental elements of *spinalatus* and *amplexicaudatus*.

Sexual dimorphism. — Andersen (1912), in his general description of the genus *Rousettus*, wrote that "females seem to average a trifle larger than males, but the difference, if any, is infinitesimal". Later authors have usually pooled the measurements of males and females. As indicated by Phillips (1968), in fact males average always larger than females. Even if this is not immediately apparent, taxonomic reports should treat the sexes separately (compare, for instance, male and female forearm lengths and greatest skull lengths in tables 1-4).

***Rousettus amplexicaudatus* (Geoffroy, 1810)**

Andersen (1912) reduced three species to as many races of *R. amplexicaudatus*: "*R. a. amplexicaudatus* (Indo-Malaya generally, excluding Java), *R. a. minor* (Java), and *R. a. brachyotis* (Austro-Malaya)."

According to his diagnoses, the most important

differences would be "[minor] as *R. amplexicaudatus*, but averaging in every respect conspicuously smaller. Similar in size to (or averaging very little larger than) *R. brachyotis*, which however differs by the greater average breadth of its cheek-teeth" (Andersen 1912).

It is our general idea that *R. amplexicaudatus* can only be divided into subspecies on the basis of size. Although a fairly large number of specimens could be studied, many of the localities (mainly islands) were only represented by a very small number of adult animals. Somewhat more extensive series were only available from Java, the Philippines, (mainland) New Guinea, the Solomon Islands, and, to a lesser extent, from Timor. At first, therefore, these five (groups of) populations were compared with each other. Using the Coefficient of Difference (Mayr 1969) as an indication, the following was evident:

1. specimens from the Solomon Islands are significantly smaller than the others
2. specimens from the Philippines and from New Guinea are mutually indistinguishable, both being relatively large
3. specimens from the Philippines and from New Guinea are significantly larger than those from Java
4. specimens from Timor (the type locality) are larger, but not significantly, than those from Java, and smaller, but not significantly, than those from Philippines/New Guinea; their similarity with the specimens from New Guinea and the Philippines, however, is greatest.

On this basis it was decided to group the populations into three geographic sections:

- a. Timor, New Guinea and Philippines
- b. Java
- c. Solomon Islands.

Specimens from other islands and localities could almost without exception be assigned to either one of these sections. We therefore propose, for the present, to recognize three subspecies, which can be provided with existing names: *Rousettus amplexicaudatus amplexicaudatus* (Geoffroy, 1810), *R. a. infumatus* (Gray, 1870), and *R. a. brachyotis* (Dobson, 1877). Their respective ranges, as far as known, will be specified in the sections on these subspecies below. The subspecific status of

the specimens from Celebes and adjacent islands must be left undecided, as will be discussed.

Rousettus amplexicaudatus amplexicaudatus
(Geoffroy, 1810)

Pteropus amplexicaudatus Geoffroy-St. Hilaire 1810: 96-97, pl. 4 (type locality: Timor; holotype MNHN; see below).

Eleutherura philippinensis Gray 1870: 119 (type locality: Manilla; holotype BMNH 1858.3.29.1).

Cynonycteris bocagei Seabra 1898: 160-161 (type locality: Dyli, Timor; holotype Museu Bocage, Lisbon, no. 2634).

Rousettus amplexicaudatus, Andersen 1912: 40-44, 811-812, 829-831 (Indo-Malaya except Java, descr., meas., synonyms); Hollister 1912: 9 (Philippines: Guimaras, Luzon, Negros, Samar); Hollister 1913: 305 (Philippines: Luzon, Lubang, Negros); Dammerman 1928: 302 (Sumba); Taylor 1934: 173-174 (Philippines, descr., meas., range); Lawrence 1939 (Philippines: range, ecology, size); Sody 1940: 391-392 (Enggano, meas.); Chasen 1940: 22 (Malay states, Enggano, Borneo, Tagoot in Burma); Laurie & Hill 1954: 31 (Sumba, Savu, Timor, Peleng); Aldridge & Cranbrook 1963: 202 (Sarawak); Harrison 1967: 229 (Niah, Sarawak; partim); Medway 1969: 10 (Selangor, Pahang, Langkawi Island); Alcasio 1971: 6 (Philippines: Luzon, Mindoro, Mindanao, Negros); Lim 1973: 6 (Pahang, ecology); Harrison 1974: 96 (Malaya, Singapore); Lekagul & McNeely 1977: 69-70 (Thailand, descr., ecology); Menzies 1977: 335 (New Guinea, subfossil).

Rousettus amplexicaudatus amplexicaudatus, Andersen 1912: 811 (Indo-Malaya); Chasen 1931: 110 (Borneo); Chasen 1940: 22, 29 (Malay states, Tennasserim, North Siam); Tate 1942: 335 (Peleng, Borneo); Forcart 1952: 180 (Sumba, meas.); Hill & Thonglongya 1972: 173 (Thailand); Medway 1977: 39 (Borneo); Goodwin 1979: 84-86 (Timor, descr., meas., habitat, ecology, reproduction).

Rousettus brachyotis, Andersen 1912: 45 (Amboina, New Guinea); Dollman 1930: 431 (Halmahera).

Rousettus amplexicaudatus brachyotis, Tate 1942: 335 (Cyclop Mt., New Guinea); Laurie & Hill 1954: 31 (Halmahera, Amboina, Buru, Ceram, New Guinea); Krutzsch 1959: 390 (New Guinea, baculum); Lidicker & Ziegler 1968: 28 (New Guinea, meas.).

Rousettus stresemanni Stein 1933 (type locality: Japen Island; holotype ZMB 44528); Tate 1942: 335 (Japen); Laurie & Hill 1954: 32 (Japen); McKean 1972: 3 (New Guinea, descr., meas.); Menzies 1977: 335 (New Guinea). New synonymy.

Rousettus amplexicaudatus stresemanni, Koopman 1979: 4 (New Guinea, Bagabag).

Rousettus leschenaulti, Wroughton 1915: 702 (Tagoot in Burma).

Known range: Burma, Thailand, Malaya, Borneo, Philippines (Luzon, Polillo, Busuanga, Palawan, Balabac, Negros, Cebu, Leyte, Samar, Mindanao), Ternate, Halmahera, Ceram, Ambon, New Guinea, Japen, Bagabag, Kisar, Timor, Roti, Ndao, Sawu, Sumba, Enggano, Mentawai.

Type specimen: Geoffroy-St. Hilaire (1810) based his *Pteropus amplexicaudatus* on "plusieurs individus de cette espèce" collected by Peron and Lesueur on Timor. Peters (1873) compared what he called "das Original-exemplar" (a skin without skull; probably the specimen figured by Geoffroy) with the type of *R. leschenaultii*. The specimen was also examined by Andersen (1912) in the MNHN collection: "a young individual, mounted, much faded, skull extracted, labelled "Timor, Exp. Baudin"; reg. no. A. 79". Recently, the specimen could not be located (Bergmans & Hill, 1980), but it is unlikely that it is lost.

Characteristics: The subspecies is characterized by its relatively large size. Selected measurements of each population are given in table 1. To some extent there is an overlap in dimensions with those of the smaller *R. a. infumatus* (see table 2), but the ranges are clearly different. Individual specimens can usually be assigned to either one of these subspecies on the basis of greatest skull length, condylobasal length, and metacarpal lengths. (In connection with the discrimination of *R. celebensis*, measurements of some premolars and molars of samples from Timor and the Philippines have been included in table 6.) The subspecies comprises many separate populations, inhabiting a large number of islands, both large and small, as listed under "known range" but probably many more. One may expect, therefore, to find some variation if individual populations are compared. Notwithstanding observed small differences we feel that the populations concerned are yet best considered as representatives of one subspecies. With the population of Timor, as *terra typica*, as reference, the other samples will be shortly discussed below.

Roti, Ndao, Sawu, Sumba. Specimens compare well with those from Timor. Absolute skull lengths possibly slightly greater (table 1), but our Timor data certainly do not cover the complete size range (compare Goodwin, 1979). The material from Sawu consists of two subadults only, and is provisionally included on the basis of geography.

Kisar. Females not different from those from Timor. The single male studied has a rather long skull.

Malaya, Thailand, Burma. From the Malayan

Table 1. Selected measurements of males and females of different populations of *Rousettus amplexicaudatus amplexicaudatus* (Geoffroy).

| | n | m | range | n | m | range | n | range | n | range | n | m | range | n | range | |
|--------------------------------|----|------------|-----------|---|-------|-----------|---|-----------|---|-----------|----|-------------|-----------|---|-----------|--|
| ♂♂ | | Timor | | | Roti | | | Sumba | | Kisar | | Philippines | | | Borneo | |
| Forearm length | 8 | 82.6 | 79.0-85.0 | 4 | 83.0 | 81.1-85.1 | 3 | 82.0-83.2 | 1 | 88.0 | 22 | 84.8 | 79.0-90.5 | 1 | 86.9 | |
| Length 3rd metacarpal | 8 | 51.6 | 48.6-53.8 | 4 | 52.8 | 50.9-55.1 | 3 | 49.2-50.5 | 1 | 53.5 | 23 | 54.3 | 50.5-57.7 | | | |
| Length 5th metacarpal | 8 | 49.1 | 47.7-51.8 | 4 | 50.0 | 46.8-52.1 | 3 | 47.8-49.4 | 1 | 50.6 | 23 | 51.6 | 47.6-55.0 | | | |
| Greatest skull length | 6 | 37.6 | 36.7-38.0 | 2 | | 37.1-38.2 | | | 1 | 39.1 | 10 | 38.3 | 37.8-39.7 | 1 | 37.9 | |
| Condylbasal length | 6 | 35.7 | 35.3-36.0 | 2 | | 35.8-37.5 | | | 1 | 37.7 | 10 | 37.0 | 35.4-38.7 | 1 | 36.5 | |
| Zygomatic width | 6 | 22.2 | 21.0-23.5 | 3 | 23.3 | 22.7-24.2 | 1 | 22.4 | 1 | 24.7 | 12 | 23.5 | 22.3-24.5 | 1 | 24.1 | |
| C ¹ -M ² | 6 | 13.2 | 12.5-13.8 | 2 | | 13.1-13.7 | 1 | 13.3 | 1 | 13.9 | 9 | 13.6 | 13.1-14.3 | 1 | 13.8 | |
| C ₁ -M ₃ | 6 | 15.0 | 14.3-15.5 | 2 | | 14.4-15.3 | 1 | 14.7 | 1 | 15.5 | 9 | 15.4 | 14.9-15.9 | | | |
| ♀♀ | | | | | | | | | | | | | | | | |
| Forearm length | 13 | 81.4 | 79.0-83.2 | | | | | | 2 | 80.5-80.7 | 22 | 84.4 | 78.1-89.0 | | | |
| Length 3rd metacarpal | 13 | 51.1 | 47.2-53.0 | 1 | | 52.2 | | | 2 | 49.2-49.6 | 23 | 52.4 | 48.6-55.7 | | | |
| Length 5th metacarpal | 13 | 48.4 | 45.6-49.8 | 1 | | 47.4 | | | 2 | 46.9-47.5 | 23 | 49.1 | 45.4-51.5 | | | |
| Greatest skull length | 10 | 36.0 | 35.0-36.4 | 1 | | 35.7 | | | 1 | 35.7 | 14 | 36.7 | 35.5-37.9 | | | |
| Condylbasal length | 10 | 34.7 | 33.8-35.3 | 1 | | 34.9 | | | 2 | 32.6-34.6 | 13 | 35.2 | 33.5-36.8 | | | |
| Zygomatic width | 10 | 21.2 | 20.1-22.0 | 1 | | 22.2 | | | 2 | 20.5-21.0 | 16 | 21.5 | 20.1-23.1 | | | |
| C ¹ -M ² | 10 | 12.9 | 12.5-13.5 | 1 | | 12.6 | | | 2 | 12.5-12.8 | 13 | 13.3 | 12.7-14.1 | | | |
| C ₁ -M ₃ | 10 | 14.4 | 13.8-14.8 | 1 | | 14.4 | | | 2 | 14.0-14.3 | 15 | 14.7 | 13.8-15.8 | | | |
| ♂♂ | | New Guinea | | | Japan | | | Thailand | | Malaysia | | Mentawai | | | Enggano | |
| Forearm length | 6 | 86.4 | 83.4-91.0 | 2 | | 84.5-89.7 | 1 | 80.3 | 2 | 82.7-85.4 | 1 | | 82.8 | 2 | 74.2-78.3 | |
| Length 3rd metacarpal | 6 | 53.8 | 52.4-56.0 | 2 | | 54.4-54.9 | | | 1 | | 1 | | 50.8 | 2 | 47.6-48.5 | |
| Length 5th metacarpal | 6 | 50.8 | 49.0-54.0 | 2 | | 51.5-51.7 | | | 1 | | 1 | | 48.0 | 2 | 47.3-48.0 | |
| Greatest skull length | 13 | 38.4 | 36.1-39.7 | 2 | | 39.0-39.7 | | | 1 | 37.9 | 1 | | ±37.5 | 1 | 37.6 | |
| Condylbasal length | 13 | 37.1 | 35.0-38.5 | 2 | | 37.7-37.8 | | | 1 | 37.3 | 1 | | ±35.8 | | | |
| Zygomatic width | 13 | 23.4 | 22.2-25.6 | 2 | | 24.1-24.4 | 1 | 23.9 | 2 | 23.2-23.4 | 1 | | 21.0 | 1 | 21.9 | |
| C ¹ -M ² | 13 | 14.5 | 12.6-14.3 | 2 | | 14.0-14.3 | 1 | 12.7 | 2 | 13.6-13.7 | 1 | | 13.2 | 1 | 13.0 | |
| C ₁ -M ₃ | 13 | 15.2 | 14.3-15.9 | 2 | | 15.7-15.9 | 1 | 14.0 | 1 | 15.4 | 1 | | 14.8 | 1 | 14.3 | |
| ♀♀ | | | | | | | | | | | | | | | | |
| Forearm length | 3 | 80.7 | 76.5-83.0 | | | | 1 | 78.2 | 2 | 70.5-78.0 | | | | 2 | 79.5-80.7 | |
| Length 3rd metacarpal | 3 | 49.5 | 47.4-52.5 | | | | 1 | 45.8 | 1 | 48.4 | | | | 1 | 51.1 | |
| Length 5th metacarpal | 3 | 45.6 | 43.7-47.5 | | | | 1 | 42.6 | 1 | 44.4 | | | | 1 | 48.7 | |
| Greatest skull length | 32 | 37.3 | 35.6-38.9 | | | | 1 | 35.3 | 1 | 33.4 | | | | | | |
| Condylbasal length | 32 | 36.0 | 34.1-37.8 | | | | 1 | 33.8 | 1 | 31.6 | | | | | | |
| Zygomatic width | 32 | 22.3 | 20.6-24.1 | | | | 1 | 21.3 | 1 | 20.6 | | | | 1 | 22.6 | |
| C ¹ -M ² | 32 | 12.9 | 12.4-13.5 | | | | 1 | 12.6 | 1 | 12.4 | | | | 1 | 12.8 | |
| C ₁ -M ₃ | 32 | 14.5 | 13.9-15.5 | | | | 1 | 14.3 | | | | | | 1 | 14.3 | |

Table 2. Selected measurements of males and females of different populations of *Rousettus amplexicaudatus infumatus* (Gray); subspecific assignation of Alor specimens provisional.

| | Sumatra | | Krakatau | | Java | | | Bali | | | Nusa Penida | | | Flores | | Alor | |
|--------------------------------|---------|------------|----------|-----------|------|------|-----------|------|------|-----------|-------------|------|-----------|--------|-----------|------|------|
| ♂♂ | n | range | n | range | n | m | range | n | m | range | n | m | range | n | range | n | |
| Forearm length | 2 | 78.8-79.2 | 2 | 77.5-80.2 | 11 | 77.1 | 72.6-83.5 | 1 | | 81.3 | 3 | 78.2 | 74.4-83.6 | 2 | 78.7-79.5 | 1 | 77.5 |
| Length 3rd metacarpal | 2 | 48.9-49.0 | 2 | 48.4-50.4 | 11 | 48.1 | 45.1-50.6 | 1 | | 50.1 | 3 | 48.9 | 46.6-51.5 | 1 | 48.4 | | |
| Length 5th metacarpal | 2 | 45.5-48.0 | 2 | 46.6-47.6 | 10 | 44.8 | 42.0-46.8 | 1 | | 47.1 | 3 | 45.6 | 42.5-48.8 | 1 | 49.7 | | |
| Greatest skull length | 2 | 34.6-±35.6 | 1 | 35.6 | 10 | 35.5 | 34.4-35.9 | 1 | | 35.7 | 2 | | 35.0-36.4 | 1 | 35.5 | 1 | 37.5 |
| Condylbasal length | 2 | 33.2-±34.0 | 1 | 34.4 | 10 | 34.1 | 32.9-35.5 | 1 | | 34.5 | 3 | 34.8 | 33.5-35.9 | 1 | 34.0 | 1 | 35.9 |
| Zygomatic width | 1 | 21.3 | 2 | 22.0-22.6 | 9 | 22.4 | 21.2-23.7 | 1 | | 21.4 | 3 | 22.5 | 21.7-23.8 | 2 | 21.2-23.9 | 1 | 23.5 |
| C ¹ -M ² | 2 | 12.0-12.5 | 2 | 12.9-13.2 | 11 | 12.8 | 11.8-13.7 | 1 | | 13.2 | 3 | 13.2 | 12.8-13.5 | 1 | 12.2 | | |
| C ₁ -M ₃ | 2 | 13.3-13.8 | 2 | 14.7-14.8 | 11 | 14.4 | 13.7-15.2 | 1 | | 14.3 | 3 | 14.8 | 14.2-15.1 | | | | |
| ♀♀ | | | | | | | | | | | | | | | | | |
| Forearm length | 1 | 77.5 | 2 | 78.4-79.5 | 17 | 76.0 | 73.1-82.0 | 4 | 72.5 | 71.4-73.3 | 4 | 74.3 | 73.2-75.8 | 1 | 75.4 | 1 | 78.8 |
| Length 3rd metacarpal | | | 2 | 48.8-50.8 | 17 | 46.9 | 43.3-52.2 | 4 | 45.0 | 44.3-46.4 | 4 | 45.1 | 43.3-47.5 | 1 | 46.6 | | |
| Length 5th metacarpal | | | 2 | 47.7-47.8 | 17 | 44.0 | 39.1-45.6 | 4 | 41.9 | 40.0-43.3 | 4 | 42.0 | 40.9-43.6 | 1 | 44.1 | | |
| Greatest skull length | | | 2 | 34.4-34.5 | 15 | 34.1 | 33.0-35.4 | 4 | 33.3 | 32.6-34.1 | 3 | 34.3 | 33.3-34.8 | 1 | 34.1 | 1 | 34.5 |
| Condylbasal length | | | 2 | 32.5-33.5 | 15 | 32.9 | 32.1-34.1 | 4 | 31.9 | 31.0-32.9 | 4 | 32.9 | 31.8-33.6 | | | 1 | 33.4 |
| Zygomatic width | 1 | 20.7 | 2 | 19.9-20.2 | 16 | 20.3 | 19.5-21.2 | 4 | 19.6 | 18.9-20.0 | 3 | 20.6 | 19.9-21.4 | 1 | 19.7 | 1 | 21.0 |
| C ¹ -M ² | | | 2 | 12.2-12.6 | 14 | 12.3 | 11.6-13.5 | 4 | 12.2 | 11.8-12.4 | 4 | 12.3 | 11.4-12.8 | 1 | 12.1 | | |
| C ₁ -M ₃ | | | 2 | 13.4-13.9 | 16 | 13.5 | 12.0-14.7 | 4 | 13.7 | 13.4-14.2 | 3 | 13.8 | 13.7-13.9 | 1 | 13.2 | | |

peninsula and Singapore, only *R. amplexicaudatus* has been recorded. In general, the skulls of these specimens are as large as in Philippine specimens, with C1-M² lengths of 13.6 and 13.7 in two males and 12.4 in a female. One female from Negeri Sembilan (HZM 48155), although adult, is comparatively small (forearm length 70.5, greatest skull length 33.4, condylobasal length 31.6) — even smaller than females of the subspecies *infumatus* from Java. The specimens from Thailand which could be studied represent *amplexicaudatus* (C1-M² male 12.7, female 12.6), while the literature not infrequently mentions *R. leschenaultii* from this country. From Burma we have only seen *leschenaultii*, but at least a few specimens from Tagoot in Southern Burma are probably referable to *amplexicaudatus* (see Hill & Thonglongya 1972). In view of the very limited material, we can only tentatively include *amplexicaudatus* specimens from Malaya and Thailand in the nominate race.

Enggano. According to Sody (1940), the Enggano specimens are "roughly intermediate" between the populations of Java and Timor. In many cases the measurements indeed fall within the overlap of these two, but in lengths of third, fourth and fifth metacarpal, greatest skull length, and rostrum length they agree much better with the Timorese than with the Javanese animals. Mentawai. The single specimen from Pagai Utara has not been recorded in the literature before. It is larger than *R. a. infumatus* from Sumatra and Java and agrees with animals from Timor (table 1), although its M¹ (3.0×1.76) and M² (2.12×1.56) are slightly longer.

Borneo. The few specimens from Borneo are but slightly smaller than specimens from the Philippines.

Moluccas. The species has been recorded from several Moluccan islands (Ambon, Ceram, Ternate, Halmaheira). Laurie & Hill (1954) mention Buru as probable extension, but this conjecture has not yet been substantiated. (The only specimen of *Rousettus* known from Aru is here included in *R. leschenaultii shortridgei*). Andersen (1912) identified specimens from Ambon as *R. brachyotis*, which, according to his opinion, would also occur in New Guinea and further east. The

two skulls from Ambon we have seen (both immature) are insufficient for subspecific identification, but they seem larger than Javan skulls of a similar age, and we think therefore but, of course, also on geographic grounds, that Moluccan animals would rather belong to *R. a. amplexicaudatus* than to *R. a. brachyotis*. Until further specimens have become available, this placement can only be preliminary.

Philippines. These animals average somewhat larger than those from Timor but, with the exception of the condylobasal length (especially in males), all measurements show a large overlap (table 1). There is certainly no statistically significant difference between the two populations, hence the Philippine ones are included here in the nominate race. The species occurs on many islands in the Philippines. Series of more than two specimens of each sex were available only from Luzon and Mindanao. These agree well with each other, and, generally speaking, also with the smaller samples from other islands (cf. Lawrence 1939). One fully adult male from Balabac (AMNH 207585) is appreciably smaller than other Philippine males (its forearm length 73.0; condylobasal length 35.4). The single female known from Balabac (USNM 477537) agrees well with the females from other localities in the Philippines. The male from Polillo (AMNH 241711) has a relatively long forearm (measured by Taylor 1934) of 89 mm, and the skull appears to be relatively long and narrow. Neither from Balabac nor from Polillo are further specimens known, and it seems premature to attach much importance to these observations in this stage.

New Guinea. The systematic position of *Rousettus* from New Guinea and adjacent islands has long been unclear. Matschie (1899) placed them in *brachyotis*. Andersen (1912) did likewise, but lowered *brachyotis* to a subspecies of *amplexicaudatus*. In this, he has been followed by most later authors (e.g. Tate, 1942; Laurie & Hill 1954; Lidicker & Ziegler, 1968). In 1933 Stein described *Rousettus stresemanni* from Japan Island; this species would be characterized by typical colours, relatively long arms and relatively strong basicranial deflection. Although Stein (1933) mentions as comparative material a series

of *amplexicaudatus* from Timor and Sumba, the measurements he published of this species appear to have been copied largely from Andersen (1912). For this study, the holotype of *stresemanni* (adult male, skin and skull) has been re-examined. Its colour is not clearly different from specimens of *amplexicaudatus* in the ZMB collection. With its forearm length of 89.7 it is somewhat, but not significantly, larger than another male from Japan, and than most known specimens from the New Guinean mainland. Its skull (greatest length 39.7; condylobasal length 37.8) agrees completely in shape with that in adult *amplexicaudatus* males (e.g. in the equally sized Philippine AMNH 160264, to which it has been directly compared). There is no reason to connect it with the African *Rousettus lanosus* Thomas, 1906 (for which Andersen (1912) erected a subgenus, *Stenonycteris*, because of its strong basicranial axis deflection) as Stein (1933) suggested.

Menzies (1977), identifying subfossil remains from New Guinea, used the mandibular tooth row length to distinguish between *amplexicaudatus* and *stresemanni*, this being the only parameter available in his material. But the ranges given by him for recent material of both species are completely overlapped by the range in his subfossils. Coincidentally, his range for *stresemanni* (14.2-15.9) does hardly differ from that measured by us in a series of typical *amplexicaudatus* from the Philippines (14.4-15.9). Hence, in our opinion, this distinction is not tenable. Koopman (1979) put *stresemanni* down as a subspecies of *amplexicaudatus* because he could not, from the material in the AMNH collection "distinguish these two alleged species on New Guinea"; he did not state, however, how the subspecies *stresemanni* would differ from the nominate race (except, perhaps, in its distribution: New Guinea, Japan and Bagabag). From our studies it is clear that *amplexicaudatus* specimens from New Guinea are not significantly larger than those from Timor and we propose to place *stresemanni* in the synonymy of typical *amplexicaudatus*.

One adult male specimen from Milne Bay, South-East New Guinea (AMNH 159030), with a greatest skull length of 36.1 and a condylobasal

length of 35.0 (forearm length about 84), is rather smaller than other New Guinean males examined. It is larger, however, than the specimens from the Bismarck Archipelago and the Solomon Islands, here both included in *R. a. brachyotis*, and therefore preliminary retained within the typical race.

Rousettus amplexicaudatus infumatus (Gray, 1870)

Eleutherura infumata Gray 1870: 118 (type locality: Flores; holotype BMNH 1863.12.26.12).

Cynonycteris minor Dobson 1873: 203 (type locality: Java; holotype Indian Museum, Calcutta; see below). New synonymy.

Rousettus minor, Andersen 1907: 509, 1912: 43-44, 811-812 (Java, descr., meas.); Thomas & Wroughton 1909: 375 (Kalipoetjang, Java).

Rousettus amplexicaudatus minor, Andersen 1912: 812 (Java); Sody 1929: 35 (Java); Dammerman 1938: 440, 1948: 321 (Java); Tate 1942: 335 (Java, Bali, characters); Chasen 1940: 22 (Java).

Rousettus amplexicaudatus, Andersen 1912: 42-43 (Alor, Flores, Sumatra); Sody 1927: 200 (Buitenzorg, Java); Dammerman 1938: 439-440, 1948: 321 (Lang Island, Krakatau, meas.); Hoogerwerf 1953: 322 (Krakatau); Bergmans & Hill 1980: 102 (Sumatra).

Rousettus amplexicaudatus amplexicaudatus, Chasen 1940: 22 (Sumatra); Laurie & Hill 1954: 31 (Flores, Alor); Krutzsch 1962: 37 (Bali, baculum).

Known range: Sumatra, Krakatau (Lang Island), Java, Bali, Nusa Penida, Flores, and possibly Alor.

Characteristics: This subspecies is intermediate in size between the large *R. a. amplexicaudatus* and the small *R. a. brachyotis*. Some important measurements of the different populations are given in table 2. Measurements of some premolars and molars of the Javanese sample are given in table 6.

Andersen (1912) wrote that the type of *Eleutherura infumata* would be similar to "a majority of examples of *amplexicaudatus*". In fact, the three Flores specimens examined (including this type) are generally smaller than typical specimens from Timor but agree well with those of the Javanese population. This applies especially to third, fourth and fifth metacarpal lengths, greatest skull length, and condylobasal length. We consider the later described Javanese *Cynonycteris minor* Dobson 1873 as synonymous with *infumatus*. The holotype of *Cynonycteris minor* was "a dried skin (perfectly adult, teeth almost unworn), in bad

state of preservation" in the Indian Museum at Calcutta (Dobson, 1878b; Andersen, 1912). The specimen is not listed, however, in the type catalogue of the Museum of the Zoological Survey of India (Khajuria, Chaturvedi & Ghoshal, 1977) — the present repository of the former Indian Museum natural history collections — and could also not be traced when Rookmaaker visited that Museum in March 1980. Dobson's original description of *Cynonycteris minor* (1873) mentions only skin characters and compares the specimen with *amplexicaudatus* and *leschenaultii* combined (i.e. Dobson's of *amplexicaudatus*) and cannot be of much use now.

The specimens from Java average larger than *R. a. brachyotis* and smaller than *R. a. amplexicaudatus*. They show a significant difference on a subspecific level from the populations of the latter subspecies inhabiting New Guinea and the Philippines, but not from Timorese animals. Although few individuals from Bali, Nusa Penida, Flores, Krakatau and Sumatra could be examined, those specimens are smaller than animals from Timor while they compare well with the Javanese sample, which is especially evident in the condylobasal length. The two known examples from Alor (both collected by A. Everett) are only provisionally assigned to this race; the female is as small as females from Java while the male corresponds with males from Timor.

Rousettus amplexicaudatus infumatus occurs on Sumatra together with *R. leschenaultii shortridgei* and *R. spinalatus*, and, as far as is known, on Java and Bali only with the former. It is known to be actually sympatric with *leschenaultii* at Kalianda on South Sumatra and in Kaliputjang on Java.

Rousettus amplexicaudatus brachyotis

(Dobson, 1877)

Cynonycteris brachyotis Dobson 1877: 116-117 (type locality: Duke of York Island; holotype BMNH 1877.7.18.3); Dobson 1878a (extended descr.).

Rousettus brachyotis, Andersen 1912: 44-45, 829-831 (Bismarck Archipelago, Solomon Islands, descr., meas.); Sanborn 1931: 11 (Ysabel, Solomon Islands, meas., dentition).

Rousettus amplexicaudatus brachyotis, Andersen 1912: 811 (Austro-Malaya; partim); Pohle 1952: 127-128 (Bismarcks); Laurie & Hill 1954: 31 (Bismarcks);

Lidicker & Ziegler 1968: 28 (Emirau, meas.); Phillips 1968: 789 (Bismarcks); Koopman 1979: 4 (Bismarcks: Tabar, Emirau, New Britain and New Ireland).

Rousettus amplexicaudatus hedigeri Pohle 1952: 127-128 (type locality: Mamamolimo, Bougainville; holotype: see below); Phillips 1968: 789-790 (Solomons, descr., meas., range, ecology); McKean 1972: 2-3 (Solomons, meas., pelage, ecology). New synonymy.

Known range: Bismarck Archipelago (New Britain, Duke of York, Tabar, Emira); Solomon Islands (Bougainville, Fauro, Choiseul, Vella Lavella, Kolombangara, Santa Ysabel, Guadalcanal, Malaita).

Characteristics: This is the smallest subspecies, but slightly overlapping in size with the geographically widely separated *R. a. infumatus*. Important measurements are given in table 3; measurements of premolars are presented in table 6.

The holotype of *Cynonycteris brachyotis* is a young adult female ("cranial ridges not yet united"; J. E. Hill, *in lit.*) and is somewhat smaller than a fully adult female from Duke of York (ZMB 5357). Both specimens are very little larger than the females from New Britain, Tabar and Emira. A male "topotype" (BMNH 1878.2.5.5), measured by Andersen (1912: 829), is larger than the two adult males from New Britain and Tabar: greatest skull length 36.2 against 32.8-33.6; C1-M2 13.0 against 11.7-11.8; C1-M3 14.8 against 13.3-13.4. Such ranges are not exceptional, however (compare tables 1 and 2), and some variation in dimensions per island population within a (sub)species inhabiting an archipelago, moreover, is to be expected. Bergmans (1979a) met a similar situation when comparing specimens of *Dobsonia anderseni* Thomas, 1914 from various islands in the region under discussion.

In 1952 Pohle described *R. a. hedigeri*, based on a single adult male from Bougainville. It would be smaller than *brachyotis*. The holotype (skin and skull) belongs to the NHMB collection (Basel) but at least the skin may not have been returned there by Pohle (Ms. Chr. Unternährer, *in litt.* 30-X-1979). In the ZMB collection we found a skin from "Mamalomimo, Bez. Buin, Bougainville" (sic) with an NHMB label (without number), which probably belongs to the holotype. The skull has not been located in Berlin and may well

Table 3. Selected measurements of males and females of *Rousettus amplexicaudatus brachyotis* (Dobson) from the Bismarck Archipelago and from the Solomon Islands, and of *Rousettus amplexicaudatus* from Celebes, Peleng and Talisai.

| | | <i>Rousettus amplexicaudatus brachyotis</i> | | | | | | <i>Rousettus amplexicaudatus, incertae sedis</i> | | | | | | | |
|----|--------------------------------|---|------|-----------|-----------------|------|-----------|--|------|-----------|--------|------|-----------|---------|------|
| | | Bismarck Archipelago | | | Solomon Islands | | | Celebes | | | Peleng | | | Talisai | |
| | | n | m | range | n | m | range | n | m | range | n | m | range | n | |
| ♂♂ | Forearm length | 3 | 74.0 | 73.1-74.6 | 12 | 73.0 | 68.6-76.0 | 6 | 82.3 | 77.5-85.6 | 2 | | 79.3-82.0 | 1 | 82.0 |
| | Length 3rd metacarpal | 2 | | 44.3-45.3 | 11 | 43.9 | 41.8-46.8 | 8 | 50.8 | 49.1-53.7 | 2 | | 50.0-53.4 | 1 | 53.8 |
| | Length 5th metacarpal | 2 | | 42.7-43.4 | 11 | 41.9 | 40.8-43.6 | 8 | 47.0 | 43.2-49.0 | 2 | | 47.1-50.0 | 1 | 48.8 |
| | Greatest skull length | 2 | | 32.8-33.6 | 8 | 32.2 | 31.5-34.0 | 3 | 36.3 | 35.2-37.4 | 2 | | 35.6-37.3 | 1 | 37.8 |
| | Condylbasal length | 2 | | 31.8-32.2 | 9 | 30.6 | 29.9-32.3 | 3 | 34.8 | 34.2-36.1 | 2 | | 34.2-36.0 | 1 | 36.2 |
| | Zygomatic width | 2 | | 19.5-23.7 | 8 | 20.4 | 18.6-22.1 | 8 | 22.2 | 21.0-23.3 | 2 | | 22.5-22.8 | | |
| | C ¹ -M ² | 2 | | 11.7-11.8 | 9 | 11.1 | 10.7-11.6 | 6 | 12.9 | 12.1-13.6 | 2 | | 12.7-13.6 | 1 | 13.3 |
| | C ₁ -M ₃ | 2 | | 13.3-13.4 | 9 | 12.7 | 12.3-13.5 | 6 | 14.3 | 13.4-14.7 | 2 | | 14.3-15.0 | 1 | 14.9 |
| ♀♀ | Forearm length | 6 | 72.2 | 66.5-78.0 | 15 | 70.7 | 67.3-72.4 | 1 | | 81.9 | 2 | | 73.7-76.4 | | |
| | Length 3rd metacarpal | 5 | 45.0 | 43.0-46.9 | 15 | 43.0 | 41.3-45.5 | 2 | | 51.8-52.8 | 3 | 47.1 | 45.2-48.0 | | |
| | Length 5th metacarpal | 5 | 42.3 | 40.0-43.8 | 15 | 41.2 | 39.8-43.1 | 2 | | 47.3-49.6 | 3 | 44.3 | 42.8-45.4 | | |
| | Greatest skull length | 3 | 32.6 | 32.4-32.7 | 10 | 31.3 | 30.1-32.6 | 2 | | 34.7-35.4 | 2 | | 35.0-35.4 | | |
| | Condylbasal length | 3 | 31.2 | 30.9-31.3 | 10 | 30.0 | 28.8-31.3 | 2 | | 33.6-33.9 | 2 | | 33.3-33.8 | | |
| | Zygomatic width | 4 | 19.5 | 18.8-20.1 | 10 | 19.5 | 18.7-20.7 | 2 | | 20.8-21.6 | 2 | | 20.2-20.6 | | |
| | C ¹ -M ² | 6 | 11.4 | 11.1-11.9 | 10 | 10.8 | 10.1-11.6 | 2 | | 12.4-12.7 | 3 | 12.3 | 11.8-12.7 | | |
| | C ₁ -M ₃ | 6 | 12.8 | 12.4-13.2 | 10 | 12.2 | 11.7-13.1 | 2 | | 13.8-14.2 | 3 | 13.8 | 13.3-14.1 | | |

be in the osteological department of the NHMB collection, from where we received no information. The holotype is relatively small and, also according to Pohle (1952), very likely not full-grown. Another, adult male from Bougainville (BBM NG 61328) is only slightly smaller than Bismarck Archipelago specimens. In general, the studied Bougainville specimens are somewhat larger than those from the southern Solomons, but consistent with what is known from the Bismarcks (although not reaching the dimensions of the mentioned "topotype" of *brachyotis*). With our present knowledge we see no reason to maintain *hedigeri* as a valid subspecies and prefer to regard it as a synonym of *brachyotis*.

Specimens of *brachyotis* are, almost without exception, smaller than those of the other subspecies here recognized. Some overlap exists in most measurements, but hardly in greatest skull length and condylobasal length. Phillips (1968) examined 41 Solomon Islands specimens and maintained *hedigeri* as a valid subspecies smaller than *brachyotis*. His concept of the size of the latter, however, was wrong. The forearm length range of 73 to 81 which he quoted from a key to

Rousettus species in Andersen (1912: 809) in fact applies to *R. amplexicaudatus infumatus* (called *minor* by Andersen); the tentative suggestion, in the same key, that *brachyotis* is of the same size as *minor* is not by far substantiated by Andersen's own factual data, nor by those of any later author. Moreover, Pohle's type of *hedigeri* is not adult, as stated by Phillips (1968), but very likely not full-grown, as stated by Pohle (1952). There may be some slight differences in average skull measurements between specimens from the Solomon Islands and those from the Bismarcks (see table 3), but larger series than those examined (in part: the same as used by Phillips) are needed to establish possible significances.)

***Rousettus amplexicaudatus*, incertae sedis**

Rousettus amplexicaudatus amplexicaudatus, Tate 1942: 335 (Peleng).

Rousettus amplexicaudatus minor, Krutzsch 1962: 37 (Celebes, baculum).

Localities: Celebes (Gorontalo; Talassa), Muna (Raha), Peleng, Talisai.

Characteristics: Measurements of speci-

Table 4. Selected measurements of males and females of different populations of *Rousettus leschenaultii shortridgei* Thomas & Wroughton, and of *Rousettus celebensis* Andersen.

| | <i>Rousettus leschenaultii shortridgei</i> | | | | | | | | | | <i>Rousettus celebensis</i> | | |
|--------------------------------|--|-------------|------|------|-----------|------|------|-----------|---------|---------|-----------------------------|------|-----------|
| | Sumatra | | Java | | | Bali | | | Aru (?) | Celebes | | | |
| | n | range | n | m | range | n | m | range | n | | n | m | range |
| ♂♂ Forearm length | 2 | 89.8-91.0 | 8 | 89.4 | 84.0-93.8 | 9 | 89.7 | 85.7-96.3 | 1 | 88.9 | 10 | 73.4 | 67.6-82.5 |
| Length 3rd metacarpal | 2 | 54.3-56.4 | 9 | 58.1 | 54.2-59.4 | 9 | 57.2 | 53.9-60.1 | 1 | 57.6 | 10 | 48.1 | 45.5-49.7 |
| Length 5th metacarpal | 2 | 53.5-54.3 | 9 | 54.7 | 52.0-56.6 | 9 | 51.4 | 50.4-57.8 | 1 | 54.0 | 10 | 46.0 | 44.4-47.5 |
| Greatest skull length | 2 | 40.4-41.9 | 5 | 42.6 | 42.2-42.9 | 8 | 42.0 | 40.3-43.6 | 1 | 42.6 | 9 | 36.5 | 35.1-38.0 |
| Condylobasal length | 2 | 39.6-41.0 | 5 | 41.4 | 40.9-41.8 | 8 | 41.1 | 39.6-42.5 | 1 | 41.1 | 9 | 34.9 | 33.9-36.3 |
| Zygomatic width | 2 | 24.8-25.8 | 10 | 26.2 | 25.5-27.3 | 9 | 26.5 | 25.7-27.6 | | | 9 | 22.7 | 20.9-25.0 |
| C ¹ -M ² | 2 | 14.3-(15.5) | 10 | 15.9 | 15.5-16.3 | 8 | 15.7 | 15.1-16.1 | 1 | 15.2 | 9 | 13.8 | 13.2-14.7 |
| C ₁ -M ₃ | 2 | 16.1-17.4 | 10 | 17.5 | 17.0-17.9 | 9 | 17.3 | 16.4-17.6 | | | 9 | 15.1 | 14.7-15.7 |
| ♀♀ Forearm length | | | 8 | 86.5 | 85.2-91.2 | 7 | 88.6 | 85.2-90.4 | | | 12 | 72.6 | 67.2-77.9 |
| Length 3rd metacarpal | | | 15 | 55.8 | 51.1-57.4 | 7 | 55.4 | 52.3-58.6 | | | 12 | 48.2 | 46.3-50.5 |
| Length 5th metacarpal | | | 14 | 52.5 | 47.9-55.2 | 7 | 52.1 | 48.9-53.9 | | | 12 | 45.7 | 43.0-47.5 |
| Greatest skull length | | | 47 | 40.3 | 38.8-42.5 | 6 | 41.4 | 40.1-42.2 | | | 11 | 35.8 | 35.4-36.3 |
| Condylobasal length | | | 43 | 39.1 | 37.3-41.7 | 6 | 40.5 | 39.2-41.5 | | | 11 | 34.5 | 34.1-35.4 |
| Zygomatic width | | | 47 | 23.7 | 21.6-25.9 | 7 | 25.2 | 24.2-26.3 | | | 11 | 21.1 | 19.9-21.9 |
| C ¹ -M ² | | | 44 | 15.0 | 14.0-16.3 | 5 | 15.4 | 14.4-15.8 | | | 11 | 13.5 | 12.7-14.1 |
| C ₁ -M ₃ | | | 41 | 16.6 | 15.5-17.5 | 5 | 17.0 | 16.2-17.7 | | | 11 | 14.8 | 14.0-15.5 |

mens from Celebes, Peleng and Talisai are given in table 3.

Probably because Andersen (1912) suggested that "the alleged occurrence [of *R. amplexicaudatus* on Celebes] probably rests on confusion with a distinct species (*R. celebensis*)", all specimens of *Rousettus* from this island have since been referred to the latter species. A series of 9 specimens from Talassa (South-West Celebes) in the AMNH collection, however, undoubtedly represents *R. amplexicaudatus*. They differ from *celebensis* in fur distribution, greater third metacarpal length, shorter rostrum length, (usually) shorter C¹-M² length, larger M²-M² width, shorter C₁-M₃ length, and teeth dimensions. Subspecific allocation of these specimens is not as easy. In cranial measurements they generally agree with Javanese *infumatus*, although in two males the greatest skull length (37.4 and 36.4, respectively) is larger than in any specimen of this subspecies we have seen, and is rather as in typical *amplexicaudatus* from Timor. Moreover, metacarpals and phalanges of third, fourth and fifth fingers are often up to a few mm longer than in *infumatus*. More specimens from Celebes are needed to analyse size ranges and classify these populations correctly. The specimens from Muna, Peleng and Talisai are also clearly *amplexicaudatus*. The only specimen from Muna is subadult. The single adult male from Talisai agrees with our Timorese sample in size. The small series from Peleng resembles that from Celebes: the three adult females measure as Javanese *infumatus* females

but the two adult males again combine characters of *infumatus* with some of the nominate subspecies as met on Timor. (One subadult male from Peleng, AMNH 109045, has short and wide molars as in *amplexicaudatus*, but its fur resembles that of *celebensis*; its metacarpals and phalanges are already longer than in any adult Timorese male. Skin and skull probably do not belong together.)

Rousettus leschenaultii leschenaultii

(Desmarest, 1820)

N.B. This synonymy includes only references relating to *R. leschenaultii* in the South-East Asian mainland (N.E. India and further to the east).

Pteropus Leschenaultii Desmarest, 1820: 110 (type locality: environs de Pondichéry; syntypes in MNHN).

Eleutherura fuliginosa Gray 1870: 118 (type locality: Loa Mountains, Siam; holotype BMNH 1862.8.18.5).

Rousettus leschenaultii, Andersen 1912: 35, 38 (Myingyan in Burma, Moulmein in Burma, India, China, Laos Mts. (sic) in Siam); Gyldenstolpe 1919: 132 (Laos Mts. (sic), Siam); Osgood 1932: 199 (Backan, N. Vietnam); Mendez 1937: 62 (Moulmein, Burma); Allen 1938: 157 (S. China); Chasen 1940: 29 (Northern Siam); Carter 1943: 105 (Kawya, Burma, meas.); Ellerman & Morrison-Scott 1951: 93 (Burma, Tenasserim, N. Siam, Tonkin, Amoy); Kao *et al.* 1962 (S. Yunnan); Wang *et al.* 1962 (S. W. Kwangsi); Marshall 1967: 63 (Hong Kong); Hill & Thonglongya 1972: 173 (Thailand); Lekagul & McNeely 1977: 71 (Thailand, range, descr., meas., ecology).

Rousettus leschenaultii leschenaultii, Phillips 1967: 633 (Laos, meas.).

Cynonycteris amplexicaudata, Swinhoe 1870: 616 (Amoy).

Rousettus amplexicaudatus, Ellerman & Morrison-Scott 1951: 93 (N. Siam, Tenasserim, Indo-China); Agrawal & Bhattacharyya 1977: 139 (Tripura).

Rousettus amplexicaudatus amplexicaudatus, Agrawal & Sinha 1973: 183 (Tripura and Burma, bacula).

Table 5. Maxillary tooth row length ranges and M₃ length ranges in males and females of *Rousettus amplexicaudatus* (Geoffroy) (all populations except South-East Asian mainland ones), and of *Rousettus leschenaultii leschenaultii* (Desmarest) and *R. l. shorridgei* Thomas & Wroughton.

| | | males | | females | | Andersen, |
|---------------------------------------|--------------------------------------|-------|-----------|---------|-----------|-----------|
| | | n | min-max | n | min-max | 1912: 830 |
| length C ¹ -M ² | <i>R. amplexicaudatus</i> | 73 | 10.7-14.3 | 107 | 10.1-14.1 | 11.8-14.2 |
| | <i>R. l. leschenaultii</i> (India) | 7 | 14.2-15.1 | 12 | 13.1-14.6 | 14.0-15.7 |
| | <i>R. l. shorridgei</i> (Java, Bali) | 18 | 15.1-16.3 | 51 | 14.0-16.3 | 16.3 |
| length M ₃ | <i>R. amplexicaudatus</i> | 64 | 1.2-1.72 | 71 | 1.0-1.68 | 1.1-1.7 |
| | <i>R. l. leschenaultii</i> (India) | 2 | 1.88-1.92 | 3 | 1.68-1.92 | 1.7-2.1 |
| | <i>R. l. shorridgei</i> (Java, Bali) | 2 | 1.92-2.2 | 23 | 1.68-2.12 | 2.2 |

Known range: India, Burma, Thailand, Vietnam, Laos, possibly Cambodia, South China, Hong Kong. Extralimital: peninsular India, Nepal, Pakistan.

Characteristics: The species is characterized by the length of C^1-M^2 and by the length of M_3 (table 5).

Andersen (1907, 1912) lists many differences between *R. leschenaultii* and *R. amplexicaudatus*. Not infrequently these differences are expressions of one and the same observation: that *leschenaultii* is the larger species of the two. Furthermore, M_3 in *leschenaultii* would be elliptical (about twice as long as broad) against a subcircular M_3 (1.2 to 1.5 times as long as broad) in *amplexicaudatus* (Andersen, 1912).

During the present study it was found that the species are best separated on the basis of C^1-M^2 length and M_3 length. Body measurements did not provide constant discriminating characters. Unfortunately, we could study but few examples from the South-East Asian mainland regions where the species are sympatric. It could be that more material from these regions will reveal that here the observed differences between the two are more apparent.

Agrawal & Sinha (1973) described bacula of specimens from Tripura, North-East India (ZSI 19426), and from Moulmein in Burma. Although both samples are identified as "*R. a. amplexicaudatus*", they probably belong to *R. leschenaultii*. The three adult specimens examined from Tripura and Arunachal Pradesh all have a maxillary tooth row length of 14.7 and for that reason they are here referred to *R. leschenaultii*. The four skulls from Burma ("Burma" and Moulmein cave) agree in size with large *R. amplexicaudatus* but they differ in the C^1-M^2 length (males 15.0 and 15.2, female 13.9) and the M_3 length (one male 2.2), which points to *R. leschenaultii*. Agrawal & Bhattacharyya (1977) state about one specimen from Tripura (again, ZSI 19426) "the specimen resembles *R. leschenaultii* in the size of the 3rd lower molar (length \times width = 1.9 \times 1.0), but resembles *R. amplexicaudatus* in the width of the ear and in the structure of the baculum, viz. hurricane-lantern shaped." As baculum shape variation is still practically un-

studied, the character may better not be used in preference over others. Unfortunately the specimens from Yado-Cassin and from Tagoot could not be identified with certainty. Chasen (1940) and Hill & Thonglongya (1972) referred other specimens from Tagoot to *R. amplexicaudatus*. All specimens from Thailand and Malaysia we could examine also represent the latter species. Those we could study from Cambodia and Vietnam (among which no adults with extracted skulls) are, with some reservation, assigned here to *leschenaultii*. Andersen (1912) identified one specimen from "Cambodia" (BMNH 7.1.1.263) as *amplexicaudatus*; knowing his criteria we think he may have been right (we only saw the skin of this specimen and can neither confirm nor reject his identification). Osgood (1932) and Phillips (1967) reported *R. leschenaultii* from North Vietnam and Laos, respectively. The specimens presently examined from Hong Kong and southern China all belong to *R. leschenaultii* in view of the M_3 length (male 2.05; females 1.8 and 1.9) and — less clearly — of the C^1-M^2 length (males 13.9 and 15.2; females 13.7 and 14.5). In the animal from Hong Kong (ZMB 352) and in two from Wutsung (ZMB 43257, -59) the notopatagium is densely furred. A similar hairiness is present in all specimens of *R. celebensis*, but has never been observed in *R. amplexicaudatus*.

It may be clear from these notes that further study of South-East Asian mainland *Rousettus* is highly desirable.

Rousettus leschenaultii shortridgei

Thomas & Wroughton, 1909

Rousettus shortridgei Thomas & Wroughton 1909: 374 (Kaliputjang, Java; descr., meas.); Andersen 1912: 811, 830-831 (Java, descr., meas.); Dietz 1916: 154 (Java meas.).

Rousettus leschenaultii shortridgei, Chasen 1940: - 22 (Java); Tate 1942: 335 (Java); Krutzsch 1962: 37 (Java, baculum).

Rousettus leschenaultii, Bergmans & Hill 1980: 103-104 (Sumatra).

Rousettus amplexicaudatus, Voûte 1968 (Java, meas.).
Xanthorpya amplexicaudata, Kohlbrugge 1913 (Java, reproduction).

Known range: Sumatra, Simeuluë, Java, Bali, ? Aru Islands. Simeuluë, Bali and Aru Is-

lands are new localities for this species. With Matschie (1899) we doubt the origin of the specimens said to be from the latter islands.

Characteristics: This subspecies is larger than *R. l. leschenaultii* but agrees with this in C_1 - M_2 length and M_3 length. See tables 4 and 5. Both single adult male specimens from Simeuluë, off the North-West coast of Sumatra (condylobasal length 39.6) and from Kalianda, South Sumatra (41.0) are somewhat smaller than specimens from Java, while some of those from Bali are larger than the Javanese ones. This supports the idea of clinal increase in size from India towards the East, as suggested by Bergmans & Hill (1980). Of course the situation in Malaya, from where *leschenaultii* has not been recorded, and in Thailand and Burma, from where very few specimens are known, may be found to interfere with this hypothesis.

The only specimen of *Rousettus* ever collected on Aru, an adult ♂, is in all its cranial measurements as large as *R. l. shorridgei*. The C_1 - M_2 length of 15.2 distinguishes it from *R. amplexicaudatus*. If the locality of this trader's specimen is correct it would greatly extend the known range of *R. leschenaultii*.

On Java, the only island from where large series of both *leschenaultii* and *amplexicaudatus* are available, the two are clearly differing in size. The

large series from Tjandi Paree referred to *amplexicaudatus* by Kohlbrugge (1913) and Vouët (1968) doubtlessly belongs to *leschenaultii shorridgei*.

Rousettus celebensis Andersen, 1907

Rousettus celebensis Andersen 1907: 509-510 (type locality: Mt. Masarang, 3500 ft, Celebes; holotype BMNH 1897.1.2.8).

Rousettus celebensis, Andersen 1912: 47 (Celebes, Sanghir); Tate 1942: 334 (Celebes); Koopman 1979: 4 (Celebes).

Known range: Celebes, Sangihe Islands (Sangihe, Siau, Tahulandang), ? Talaud Islands.

Characteristics: The species is characterized by the combination of its fur distribution and its teeth dimensions. See for measurements tables 4 and 6.

According to Andersen (1907), this species is distinguished from what is now called *R. amplexicaudatus brachyotis* by its "larger skull, very narrow palate, narrow molars, not deciduous P^2 [= P^1], much longer pollex, longer wings (chiefly owing to the longer metacarpals), much longer fur, haired notopatagium, and much more densely haired tibiae." The differences in hairiness, especially the absence of a reduction of hairs in the neck region, the furry notopatagium, and the greater length' of the hairs if compared to both *R. amplexicaudatus* and *R. leschenaultii* are very

Table 6. Length and width ranges of P^4 and molars in selected populations of *Rousettus amplexicaudatus amplexicaudatus* (Geoffroy) (Timor, Philippines), *R. a. infumatus* (Gray) (Java), *R. a. brachyotis* (Dobson) (Solomon Islands), and of *Rousettus celebensis* Andersen.

| | <i>R. a. amplexicaudatus</i> | | | | <i>R. a. infumatus</i> | | <i>R. a. brachyotis</i> | | <i>R. celebensis</i> | |
|--------------|------------------------------|------------|-------------|-------------|------------------------|-------------|-------------------------|-------------|----------------------|-------------|
| | Timor | | Philippines | | Java | | Solomons | | Celebes | |
| | ♂ n = 4 | ♀ n = 8 | ♂ n = 12 | ♀ n = 19 | ♂ n = 8 | ♀ n = 19 | ♂ n = 10 | ♀ n = 10 | ♂ n = 2 | ♀ n = 10 |
| P^4 length | 2.32-2.64 | 2.28-2.6 | 2.4-2.64 | 2.2-2.6 | 2.48-2.6 | 2.2-2.52 | 1.8-2.2 | 1.84-2.04 | 3.0-3.08 | |
| width | 1.36-1.8 | 1.52-1.84 | 1.44-1.88 | 1.4-1.88 | 1.56-1.8 | 1.52-1.96 | 1.44-1.72 | 1.4-1.64 | 1.6-1.72 | |
| M^1 length | 2.44-2.92 | 2.44-2.84 | 2.52-3.0 | 2.28-2.88 | 2.52-2.68 | 2.28-2.76 | 2.1-2.48 | 1.8-2.4 | 2.5-2.9 | 2.6-2.9 |
| width | 1.6-1.8 | 1.52-1.84 | 1.6-1.8 | 1.6-1.88 | 1.52-1.68 | 1.52-1.92 | 1.48-1.76 | 1.28-1.68 | 1.3-1.6 | 1.3-1.5 |
| M^2 length | 1.7-1.92 | 1.6-1.8 | 1.84-2.08 | 1.76-2.2 | 1.64-2.0 | 1.64-1.92 | 1.48-1.88 | 1.48-1.72 | 1.4-1.64 | |
| width | 1.36-1.6 | 1.28-1.48 | 1.36-1.68 | 1.36-1.96 | 1.32-1.44 | 1.2-1.56 | 1.3-1.56 | 1.24-1.52 | 1.1-1.2 | |
| M_1 length | 2.4-2.72 | 2.36-2.72 | 2.4-2.76 | 2.32-2.76 | 2.4-2.56 | 2.24-2.56 | 2.0-2.4 | 2.0-2.28 | 2.76-2.9 | |
| width | 1.48-1.6 | 1.28-1.6 | 1.4-1.72 | 1.32-1.6 | 1.4-1.56 | 1.32-1.6 | 1.32-1.58 | 0.92-1.56 | 1.3-1.4 | |
| M_2 length | 1.9-2.2 | 1.92-2.16 | 1.8-2.32 | 1.92-2.32 | 2.0-2.2 | 1.84-2.12 | 1.8-2.16 | 1.72-1.96 | 2.1-2.16 | |
| width | 1.36-1.5 | 1.24-1.52 | 1.36-1.6 | 1.32-1.6 | 1.32-1.52 | 1.24-1.48 | 1.28-1.48 | 1.24-1.44 | 1.2-1.24 | |
| M_3 length | 1.4-1.6 | 1.04-1.48 | 1.4-1.72 | 1.28-1.68 | 1.2-1.72 | 1.24-1.52 | 1.24-1.52 | 1.12-1.32 | 1.3-1.44 | |
| width | 0.96-1.2 | 0.8-1.12 | 0.96-1.24 | 0.96-1.24 | 0.84-1.16 | 0.8-1.08 | 0.96-1.12 | 0.76-1.0 | 0.9-1.0 | |

distinct in all specimens examined. From the few available data on collecting altitudes (see the section Specimens examined) it does not follow that this hairiness is an adaptation to climatic conditions, i.e. lower temperatures. The metacarpals and phalanges of all fingers are long in comparison with Andersen's "*R. brachyotis*", but they agree in size with his "*R. amplexicaudatus*". The size of the skull is comparable to large specimens of *R. a. infumatus* or to small specimens of *R. a. amplexicaudatus*. *R. celebensis* however, has a relatively longer rostrum, longer lower and upper tooth rows and a smaller average distance between the two M^2 . The tooth rows run practically parallel (as opposed to a posterior divergence in *amplexicaudatus*). The size of the molars seems to provide the best distinguishing characters, although the teeth could only be measured in a small number of specimens of *R. celebensis*. In comparison with *R. a. amplexicaudatus* and *R. a. infumatus*, P^4 is longer; M^1 is narrower; M^2 is shorter and narrower; M_1 is longer and narrower; M_2 is narrower; and M_3 is sometimes shorter and narrower (table 6). These tooth size differences are less clear between *celebensis* and *amplexicaudatus brachyotis*. The latter subspecies is relatively small and consequently often has shorter and narrower cheek teeth than the other subspecies.

Rousettus celebensis and *R. amplexicaudatus* are sympatric in the environs of Gorontalo.

***Rousettus spinalatus* Bergmans & Hill, 1980**

Rousettus spinalatus Bergmans & Hill 1980: 95-104, figs. 1-5 (type locality: Northern Sumatra (either in or near Medan, or in or near Prapat); holotype in Naturhistorisches Museum, Vienna, no. 24112).

Rousettus amplexicaudatus, Harrison 1967: 229 (partim: the specimen collected 6-XI-1965; Niah, Sarawak).

Known range: Northern Sumatra, Western Borneo.

Characteristics: This species is easily recognized by its high wing insertion and a number of dental characters, for the details of which the reader may be referred to the original description. Specimen ZRCS no. 7188 from Ulu S. Pandan, Bintulu, Sarawak, a new locality, is the fourth known specimen of this recently discovered species

and the second specimen known from Borneo. It has been compared directly to the holotype specimen and essentially agrees in all respects. As it is only the second adult specimen its measurements (all taken by Bergmans) are given.

Forearm length 89.3, external tail 9, ear 15, hindfoot 19, tibia about 34.5, 3rd metacarpal 51.2, 5th metacarpal 47.5; greatest skull length 35.9, condylobasal length —, rostrum length 12.0, palatal length 18.3, cranium width 14.9, interorbital width 8.4, postorbital width 7.7, zygomatic width —; width over cingula C^1-C^1 7.0, C^1-M^2 12.9, M^2-M^2 10.8, C_1-M_3 14.3; length \times width P^3 2.25 \times 1.4, P^4 2.4 \times 1.9, M^1 2.7 \times 2.0, M^2 2.0 \times 1.6, P_3 2.0 \times 1.25, P_4 2.2 \times 1.6, M_1 2.4 \times 1.6, M_2 2.3 \times 1.6, M_3 1.8 \times 1.2; distance between M^2 and palate margin (see fig. 4 in Bergmans & Hill, 1980) 0.8.

The specimen is larger than the holotype (which has a forearm of 80.6). This may be an indication of body size variation, but also of possible differences between Sumatran and Bornean populations. In this connection it is interesting to note that its cheek teeth are generally slightly broader than those of the holotype, just as those of the other known Bornean specimen. Unlike the latter, it agrees with the holotype in the absence of fur on the middle neck and in between the shoulders. It also has a high mandible (height 0.47% of length) which may be an additional specific character distinguishing *spinalatus* from *amplexicaudatus* (cf. Bergmans & Hill, 1980).

? ***Rousettus* species**

Aldridge & Cranbrook (1963) described two broken mandibles of later upper Pleistocene age from Niah, which they believed to represent *Rousettus*. The specimens are smaller than any of the 32 mandibles from the same site which these authors assigned, with some reservation, to *R. amplexicaudatus*. As one of the features of these specimens they emphasize the fact that canine and cheek teeth must have been either in contact or else very close. In our opinion this probably just indicates juvenility. Of the teeth that have remained, however, M_3 measures 1.0 \times 0.7 (length \times width), which is smaller than any *amplexicaudatus* M_3 we measured (smallest: 1.16 \times 0.88; 1.16 \times

0.92; 1.2×0.84 ; 1.24×0.8), and much smaller than M_3 in *R. spinalatus*. If the generic allocation and the M_3 measurement are correct, the involved form may deserve taxonomic distinction. For this purpose, however, more complete specimens are desirable.

DENTAL ANOMALIES

We think it useful to note here the dental anomalies encountered during this study as this information may help prevent identification problems. Normal upper dentition in *Rousettus* consists of 2 incisors, 1 canine, 3 premolars and 2 molars on each side; lower dentition is the same except for an additional molar.

In *Rousettus amplexicaudatus* we found the following:

I³: present on both sides in RMNH 28270 (Java), smaller than other upper incisors, touching I², slightly separated from canines, almost completely embedded in premaxillaries, probably not visible during live.

P¹: absent on both sides in HZM 48155 (Malaya); absent on right side in MZB 122/38 (Nusa Penida).

P²: present on right side in MZB 172/39 (Java); about the size of P¹; possibly an accidental outgrowth rather than a true P².

M³: present on right side in BMNH (Malaya), ZMA 14.414 (Philippines), and MVZ 43259 (New Guinea).

M₃: absent on both sides in RMNH 28254 (Flores).

M₄: present on both sides in AMNH 207496 (Philippines); on left side only in MVZ 141110 (New Guinea).

In *Rousettus leschenaultii*:

P¹: absent on both sides in ZMB 43259 (China).

M³: present on both sides in ZMB 39608 (Sumatra).

ECTOPARASITES

Some fleas, flies and mites have been collected from the bats examined and identified as follows.

SIPHONAPTERA

Thaumapsylla breviceps Rothschild, 1907 from

Rousettus amplexicaudatus from Nikiniki, Timor (NHMB 4893).

Thaumapsylla longiforceps Traub, 1951 from *Rousettus amplexicaudatus* from Nikiniki, Timor (NHBM A4897) and from Longison Island, British North Borneo (ZRCS 7190-95).

NYCTERIBIIDAE

Eucampsipoda inermis Theodor, 1955 from *Rousettus amplexicaudatus* from Samar, Philippines (ZMB 10198), and from Longison Island, British North Borneo (ZRCS 7191).

Eucampsipoda latisterna Schuurmans Stekhoven, 1938 from *Rousettus leschenaultii* from "Indo-Chine (Saigon?)" (MNHN), and from ? Aru Islands (doubtful locality; ZMB 4412).

Eucampsipoda penthetoris Theodor, 1955 from *Rousettus leschenaultii* (one of the MNHN specimens: locality either "India", or "Indo-Chine (Saigon?)" or Angkor Vat, Cambodia).

ACARINA

Ancystropus taprobanicus (Turk, 1950) from *Rousettus amplexicaudatus* from Guadalcanal, Solomon Islands (NHMB 4150-57).

DISCUSSION

The present treatment of *Rousettus amplexicaudatus*, i.e. its subdivision into three geographically separated groups to which on the basis of dimensional characteristics subspecific ranks have been attached, seems the only procedure which our collected information allows. It more or less builds on traditional views, although geography is credited the important role it deserves — which has hopefully led to an acceptable interim concept — and necessarily mirrors our still fragmentary knowledge. This knowledge, we feel, nevertheless justifies the four statements made in the section on *R. amplexicaudatus* sensu lato (p. 12) on which its subspecific taxonomy as here proposed is based.

The majority of known populations, each restricted to one (or a few) mutually more or less isolated islands, is represented in collections by a very small number of specimens. If larger samples from these populations would become available it would not surprise us if more problems will arise as to the subspecific identity of certain populations than we already encountered

(e.g. the Celebes specimens). The distinction of subspecies may eventually become impossible, while at the same time individual island populations may be found to possess a set of characters distinguishing them from many of the others.

As regards sympatric *Rousettus* species, there should be no problem to distinguish *amplexicaudatus* from these (and these from each other, for that matter). *R. amplexicaudatus* has been confused with *R. leschenaultii* a number of times, but using the C^1-M^2 and M_3 lengths this is not necessary. The species are known to be sympatric on Sumatra, Java and Bali. Certainly on the latter two islands there is also a distinct difference in overall dimensions. From Sumatra too few specimens are known to be sure of this; as *leschenaultii* there may be smaller than on Java the difference in size may be less distinct.

Only *amplexicaudatus* is known from Malaya, but in Burma and Thailand both *leschenaultii* and *amplexicaudatus* do occur. There is no evidence as yet that they live here side by side but then, very few *Rousettus* from these regions have come to light anyhow, and actual sympatry is not unlikely. From the few available specimens it appears that *amplexicaudatus* from Burma and Thailand may equal those from the Philippines in size (thus, they are relatively big), while *leschenaultii* may overlap strongly with *amplexicaudatus*. So far, the diagnostic C^1-M^2 and M_3 lengths have sufficed to distinguish between the two species here, but otherwise they are very similar. If one could think of ecologically induced character displacement to explain the conspicuous size difference between the two species on Java, Bali and possibly Sumatra, where *amplexicaudatus* is smallest and *leschenaultii* largest, this diverging mechanism has not (yet?) acted in the South-East Asian mainland.

ADDENDUM

During the final stage of this paper we received a small collection of *Rousettus* from the ZRCS collection. Some data could still be inserted: all the specimens appear in the section Specimens examined, and notes on a specimen of *R. spinalatus* are given in the taxonomic section. The specimens of *R. amplexicaudatus* and *R. leschenaultii*,

however, have not been considered in the sections on those species and their measurements have not been included in the tables. In so far as the specimens provide useful new information this follows below. Unfortunately, several are juvenile, while most adults are in alcohol with skulls inside and with broken forearms.

Borneo: One adult male from Longison Island (7192) with forearm length 80.6, condylobasal length about 34.1, C^1-M^2 length 13.4 and M_3 length 1.38; one adult female from the same locality (7195) with C^1-M^2 length 13.8 and M_3 length 1.60; and one adult female from Kubonatok Cave (7183) with forearm length 78.7, are all *Rousettus a. amplexicaudatus* (just as the others from these localities). The male has a small skull, if compared to those examined from the Philippines (see table 1), but there is as yet no reason to doubt its subspecific status.

Burma: One adult female from Tagoot (795/16) with forearm length about 81.8, condylobasal length about 34.0, C^1-M^2 length 12.4 and M_3 length 1.33 is clearly referable to *R. a. amplexicaudatus* (compare Hill & Thonglongya, 1972).

Malaysia: One adult male from Batu Caves (7187) with forearm length 78.0, one adult female from that locality (918/11) with forearm length 83.2, greatest skull length 35.4, condylobasal length 34.3, C^1-M^2 length 13.8 and M_3 length 1.6 (and another incomplete skull of unknown sex, 909/11, from Batu Caves) also represent *R. a. amplexicaudatus*.

Thailand: One adult male from Chiangmai (7189) with forearm length 82.8, greatest skull length 36.7, condylobasal length 35.1, C^1-M^2 length 13.4 and M_3 length 1.60 keys out as *R. a. amplexicaudatus*. One adult female from Ban Na Sao, South Siam (7218) with forearm length 77.0, greatest skull length 38.0, condylobasal length 36.6, C^1-M^2 length 14.4, and M_3 length 1.92 belongs to *R. l. leschenaultii*.

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